ANNALS OF THE NEW YORK ACADEMY OF SCIENCES
Volume XLVI, Art. 10. Pages 993–1122

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BRAIN AND BODY WEIGHT IN MAN: THEIR ANTECEDENTS IN GROWTH AND EVOLUTION

A Study in Dynamic Somatometry

By

Earl W. Count

NEW YORK
Published by the Academy
January 15, 1947

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EARL W. COUNT

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* Publication made possible through a grant from the Viking Fund and the Annals Revolving Fund.

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PREFACE

During the past half-century, the growth of the human brain and the changing relations of brain weight to body weight, both in man and other animals, have been investigated by numerous authors, notably Dubois, Lapicque, Donaldson, Brummelkamp, von Bonin, and many others. But, while these studies have established many facts, the underlying principles have not yet been fully revealed. My own studies have approached the classic problem of the relations of brain weight to body weight from the direction of physical anthropology, with the results set forth in the present paper.

For the most part, the data were brought together in the American Museum of Natural History, where I am under obligation to many, and very especially to Dr. W. K. Gregory. Dr. H. B. Latimer of the University of Kansas did me the extraordinary favor of copying his extensive and unique series of measurements on body and brain weights of fetal and adult cats. I wish also to thank Dr. R. W. Miner for his editorial work in preparing the manuscript for printing.

Acknowledgment is due Miss Lillian Guglielmi, Secretary of the Department of Anatomy, New York Medical College, for typing the manuscript.

I am especially grateful to President R. C. Hunt and Dr. Paul Fejos, Director of Research, both of the Viking Fund, Inc., for their sustained interest in this work, and jointly to the Viking Fund and The New York Academy of Sciences for defraying the expenses of publication.

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SECTION I. INTRODUCTION

Our general subject is that of the relationship between brain weight and body weight in man. More accurately, we are inquiring whether the relationship in man is at all peculiar and aberrant, with respect to all his relatives in the mammalian class, or whether he fits into a common scheme.

This question breaks down into three problems:

(1) How does brain weight grow with respect to body weight, during the entire period of development of the individual? This is a question of developmental anatomy, from embryo to adult.

(2) How has brain weight changed with respect to body weight during man's evolution, starting at a time when his ancestors were in no wise separable from those of other modern primates? This is a question of paleontology.

(3) What regularity is there, if any, in the pattern obtaining today among mammals; *i.e.,* can a scheme be found which places man, with respect to the brain weight/body weight ratio, in a position understandable in the light of the positions of all other mammals? This is a question of comparative anatomy.

It is no longer disputed that these questions are mutually related. The present study seeks the way to a law, expressible in number, that will describe the relationship.

A hundred years ago, only the first and third questions would have been asked. Today, both the first and third are subordinated to the second, for reasons well known to every biologist. However, unfortunately, we still lack the kind of data that could turn this study into an attempt to answer the second question. Therefore, we shall pursue questions one and three, with the faith that any answer to them will furnish ground work for an eventual answer to question two.

A. ORIENTATION

The objectives of the present study are: (1) To formulate the growth behavior between brain and body weights in human ontogeny; (2) to find any traits in common with other Primates and Mammalia; (3) to formulate analogous behaviors in comparative anatomy; and (4) to search for any connections between ontogeny and comparative anatomy.

1. The salient features of the ontogenetic aspects: Where Y = log brain weight, X = log body weight, A = log a; both fetal and postinfantile growth behavior fit $Y = A + bX$, as a first approximation; b being much greater, and A being much smaller, in the fetal case than in the other. A transitional curvature connects the two. The sexes are formulated separately.

2. Man is compared with apes, monkeys, cattle, cats, and rats. The factors determining ultimate weight and proportion of brain to body are: (a) Its relative growth velocity before the fetus stage; (b) velocity during the subsequent period, for which we have data; (c) the amount of growth energy expended by the total body per morphological stage achieved; (d) the length and (e) degree of curvature to the line of the transitional period; (f) the length and (g) velocity of the line of postinfantile growth.

Man and ape may together be superior to the monkeys in point (a). They may be slightly superior in point (b), but this is more distinctive of the primates together with respect to the other mammals studied. Man stands highest in point (c), the apes are next, the monkeys third. The apes are highest in point (f). In point (g), the lowest velocity is that of the apes; then comes man; then the monkeys. Apes and man together are distinctive in point (g), while the monkeys resemble other mammals.

3. The salient features of the comparative anatomical aspects, assuming the Insectivora to represent the "mother order" of the extant mammals: (a) The Dubois formula $E = kP^r$ for relating brain weight to body weight is considered invalid. (b) The von Bonin formula (a rectilinear regression as a statistical mean for the whole mammalian class) is considered to fail also, but for a different set of reasons. (c) (1) Treating the mammals separately by orders, each order apparently describes, in terms of log brain weight Y and log body weight X, a parabola $Y = A + bX - cX^2$. (This is termed the "cephalization exponent.") So does the surviving mass of the class Mammalia. (2) The constants b and c are, in every instance, characteristic; but when all instances are assembled, there emerges the relationship $c = f(b)$, where $f(b)$ is rectilinear and negative, and the correlation $r_{bc} = -.912$. (3) The extant reptilian behavior is $Y = A + bX + cX^2$; and b, c agree with the mammalia in $c = f(b)$. (4) The intersection of the reptilian exponent with the general mammalian can be used as the

origin of a new pair of axes, to which all exponents can be referred, thus making $A = 0$. Then, the mammalian exponents can be treated as *transformations* out of the reptilian.

4. The salient features of the ontogenetic and comparative anatomical aspects, when juxtaposed: (a) For a major period of fetal growth, the ontogenetic line approximately parallels the comparative-anatomic (in the orders studied), although the evaluation of the former, rectilinearly, and the latter, parabolically, at the outset precludes complete parallelism (the parabolas in this stretch are gradual); (b) the fetal ontogenetic line tops the comparative-anatomic, so that, per total body weight, the fetus has devoted a larger percentage to brain weight than a putative phyletic ancestor of like body size, indicating the prefetal period as largely responsible for the precocity of brain weight; (c) the steeper the fetal ontogenetic and the comparative-anatomic lines, the greater this precocity; (d) man is not aberrant, but a quite orthodox projection to a larger absolute size of a phylogenetic formula applying equally well to the monkeys, both New and Old World.

A principle underlying all mammalian cephalization is: Increase in absolute body size is a requisite for higher cephalization.

B. STANDPOINT AND METHOD

When an anthropologist measures the body of man and compares its proportions in terms of indices, he commits himself in two ways: He pledges himself to the operations of numbers; or, he assumes an attitude towards the object of his scrutiny.

The pledge is often hard to keep. The ways of the mathematical country are very unexpected, and the traveler finds himself unequipped for rough going. Too frequently, he stops far short of where he might go, either because he finds himself unready or, alas, because he may not be aware of what good things lie beyond.

By far the bulk of anthropometric studies are content with measurements of a particular *state* obtaining for an individual or a group. They may, however, go beyond: they may register and collect, at suitable, successive intervals, the stages of growth for an individual or for a population. By interpolation, a continuum can be filled out. It can be graphed as a curve. Occasionally, the student describes the curve in terms of a formula (empirically). But commonly, the practice is to seek the average of a ratio—the average of an index—for a population at but one (usually definitive) stage of its somatic proportions. Now, ideally speaking, an index can be plotted on a Cartesian grid in terms of its component measurements, y and x. It is a point. Its only property is position, a perfectly static matter. But how did it get there? Clearly, by tracing a locus. That took time. Explicitly or implicitly, time is there as a parameter. If, now, we can formulate a locus, we have passed from a static to a dynamic method. This is right and proper, for anatomy itself is a process, not just a state. Its behavior is an event. An index, therefore, should be a locus, not a point; a formula in the variables (y, x), or (writing time as t) in (y, t) or (x, t).

To put it more technically: Let an organism grow from embryo to adult. Let a chosen set of stages be represented as:

$$A_1 - B_1 - C_1 - \ . \ . \ . \ Z_1,$$

and plotted.

Let Z be the adult. Let it be understood, however, that there is a continuum between the stages and that the stages are artifices of choice.

Let this organism be an ancestor to a later form with subscript having its homologous set of ontogenetic stages:

$$A_2 - B_2 - C_2 - \ . \ . \ . \ Z_2.$$

Let there be n such phyletic stages, so that the modern form is:

$$A_n - B_n - C_n - \ . \ . \ . \ Z_n.$$

Let us plot all Z's. We find that they conform to a pattern, to a formulable line. Yet Z_1 did not give rise to Z_n. There is no continuum between Z's, as there has been in the other case. It is the germ plasm of the organism with subscript $_1$ that eventuated in the organism with subscript $_n$ by a phylogenetic process. If, instead of Z's, our fossil records housed the stages A, C, or H of a phyletic line, we could make just as legitimate comparisons. However, the formula for the line connecting all C's would not have the same constants as that connecting all H's.

We could, if we had all stages, construct a master-chart in which we connected every A-B-C- . . . Z series with lines, and also every letter-plus-subscript series A_1-A_2-A_3- . . . A_n, etc., with another set of lines. The first would be ontogenetic; the second, phylogenetic. The one set of lines would cut across the other. With such a gridlike chart, we could visualize the gradual *distortion* of an organism during its ontogeny, or of a phyletic line during its evolution.

It is safe to say that this will never be possible. Nevertheless, I hope the belief is not too sanguine that, out of today's qualitative anatomy, with its facets paleontologic, developmental, or comparative in any other form, there will gradually emerge a quantitative anatomy of analogous syncretism, in which *processes* and *form changes* will be patiently measured and formulated, until reasonable reconstructive extrapolations or interpolations can be made that will further the accuracy of our evolutionary descriptions. It is hoped that the present study will do its bit in that cause.

C. PRINCIPLES AND TERMINOLOGY

1. The plotted points in a graphed field (the "scatter diagram") will be called a *constellation.*

2. If a constellation shows some general organization, a tendency or trend, as though streaming in some direction, we shall speak of an *orientation,* and the line of means of that orientation as the *axis.* The more pronounced the tendency to orient, the higher the correlation of the variables. We may say, then, that the line of mean or mass tendency indicates the *dependence* of one variable y upon the other x, while the amount of dispersal or scatter gives the degree of *independence* between the two.

3. We shall examine constellations of genera, families, orders, and the class Mammalia. The more comprehensive the constellation, the more pronounced the tendency for y to depend upon x, the more clearly defined the orientation. The reason is not hard to see. The total mammalian constellation is comparatively long and narrow; a species constellation will usually be short and relatively broad. Biologically interpreted, in a species or genus the range of brain size is larger, relative to the range in body size, than in an order or the class.

4. When we come to treat of comparative anatomy, we shall examine, first, the system developed by Dubois, Lapicque, Brummelkamp, *et al.,* and accepted and further exploited by others. The system claims for all vertebrates, no matter what their proportion of brain to body weight, a certain constant feature termed the "relational exponent," and a certain feature that varies according to the degree of "cephalization"; *i.e.,* in every vertebrate, the brain weight, y, is related to body weight as $y = ax^b$, where $b = .56$ and is the relational exponent; while a varies according to the "cephalization" of the animal, and is termed the "coefficient of cephalization."

We shall present the counterposed system of von Bonin, and shall attempt to analyze both. In the end, we shall propose another system, one having a "cephalization exponent," and in which the brain and body weights shall be related as $y = ax^{b\ c \log x}$. We shall then explore the consequences of its adoption.

The procedure really is simple. We start with man. Frankly, he remains, throughout, the center of interest—human egoism carried over into science. But, in part, we redeem the reproach by widening the angle of vision to include the rest of the primates. Eventually, we set the scope to sweep in other orders. In the phylogenetic section, we can, at last, see the class Mammalia; anyway, the remnant that still survives. And beyond, we catch a glimpse of the reptilian background. We start with ontogeny (Section II), then switch to comparative anatomy (Section III), and finally essay a comparison of the two (Section IV).

SECTION II. ONTOGENY

A. THE CHARACTER OF THE DATA

Using brain weight at all is, at best, an uncertain procedure. The data come from a wide range of sources, which means strong individualism in securing them. The brains may have been weighed fresh, or after various periods of preservation in all sorts of solutions. They may even have been severed at different levels. This factor can be weighty when the brains are very small. Brains will have been weighed with or without meninges, the cisternae more or less drained. Even under ideal circumstances, it still would be uncertain just how much living substance a brain weight would represent. Aside from the varying amounts of blood in the small vessels, the age and kind of animals means varying amounts of water, although this criticism would touch body weight, as well. Also, there are individualisms in the techniques of weighing which may be very important, especially when small brains are being weighed.

If brain weight is an uncertain datum, so is body weight. Some animals are well fed, others emaciated. Monkeys, for one group, are notorious gluttons when they have a chance. Stomach and intestinal content sometimes are an astounding percentage of gross body weight.

In the case of man, the data come from the least representative members of the species—the minority who have died prematurely. Disease reduces body weight, but brain weight much less profoundly. This is very important in studies limited to man. The importance is enhanced when the human are compared to animal data having another set of antecedents.

The kind of data limits their quantity and extent. (If our problem were popular, it would lead to an appalling slaughter of the "lesser creation.") Sometimes, in fact, the series for an animal is limited to one specimen. There are no real brain weights at all for *Sinanthropus* or *Homo rhodesiensis*, nor any body weights, either. If we were to substitute cranial capacity, the horizon would immediately recede a distance.

Cranial capacity, to be sure, may be used to estimate the weight of the brain it once contained. But aside from the technical difficulties preventing, in their turn, a standardized measure, one cannot be sure of the modulus by which to turn the cubic centimeters into grams. In closely related forms, like *Pithecanthropus* and *Homo,* a collateral study of living primates may permit a fairly safe judgment in the matter. However, when the range of comparison is widened taxonomically, uncertainty increases.

Also, if one is studying the *Palaeanthropi,* etc., one must estimate body weight as well.

All of these bafflements have resulted in some students advocating the use of cranial capacity, nevertheless, as the lesser of two evils. The students of fossils go further, since they have, at best, only bones from which to try recovery of body weight. Hauger (1921), for instance, has experimented with a quantity obtained from the combined volume of right humerus, radius, ulna, femur, tibia, and fibula. Using Australians, Europeans, and a scattering of others, he has obtained results that parallel what he might have gotten from body weights. However, this sort of thing has the vice of its own virtue. As a technical matter, it demands that the collector of fresh material clean all of these bones. Often that is highly impracticable.

Accordingly, we have dealt only with brain and body weights. Some data do exist. They may be far from uniform in quality or quantity, but one thing is certain: when they are put through a process, they do tell a story.

B. THE RANGE OF THE MATERIALS

1. Perspective

They are fetal and postnatal. I have tabulated raw data, straight through from the earliest obtainable up to, and (sometimes, but not always) including, adults. It will develop that, in each case-subject, the entire stretch available for a fetal period could be used for a single formula.

However, in the postnatal life, only those after some period of "infancy" could be used safely in a single formula. Accordingly, I have formulated growth curves for a life-stretch that is "postinfantile," and which terminates at adulthood. Between birth and this last period, all animals trace transitional growth curves which demand special treatment. Where to begin and where to break off is no certain matter. (For safety's sake, I have formulated the human "postinfantile" stretch from data not earlier than the age of 4. For the macaque, I have included the stretch from the beginning of permanent-tooth eruption to its completion, but not beyond. This difference of standard has no perceptible effect upon the formulations of the curves.)

The tables, then, will include some data which were not used in the formulae. Nevertheless, usually they have been plotted in the figures. The reason will be obvious on each occasion.

2. Index of Data

(1) ***Homo***	(a)	*Fetal:* 1. Composite series from Cruikshank and Miller (1924), Giese, and Rüdinger (both *fide* Cruikshank and Miller).
		2. The averages of Michaelis (1906).
	(b)	*Postnatal:* 1. Composite of Michaelis (1906) and Wendt (1909).
		2. Collaterally, tables 8 and 27 of E. Boyd (1942).
(2) ***Pan***		*Postnatal:* Data from various sources assembled by Anthony (1928), including his own.
(3) ***Simia***		*Postnatal:* Composite of Anthony (1928) and Hrdlicka (1925).
(4) ***Rhesus***		*Postnatal:* Zuckerman and Fischer (1927).
(5) ***Semnopithecus***	(a)	*Fetal: S. maurus*—Hulshoff-Pol, *fide* Anthony (1928).
	(b)	*Postnatal: S. obscurus*—Keith (1895).
(6) ***Felis***	(a)	*Fetal:* H. B. Latimer, unpublished.
	(b)	*Postnatal:* Ziehen (1901); also, Anthony (1928).
(7) ***Mus***		*Postnatal:* Donaldson and Hatai (1911).
(8) ***Ovis***	(a)	*Fetal:* Ziehen (1906).
	(b)	*Postnatal:* Crile and Quiring (1940).
(9) ***Bos***	(a)	*Fetal:* Ziehen (1906).
	(b)	*Postnatal:* Crile and Quiring (1940).
(10) ***Sus***		*Fetal:* Ziehen (1906); also, L. G. Lowry, *fide* Anthony (1928).
(11) ***Equus***		*Postnatal:* Crile and Quiring (1940).

3. Index of Tables

Brain and Body weights of:

Table

1. Human fetuses (figures 1, 2, 4, 28).
2. Chimpanzee (figures 4, 6, 28).
3. Orang (figures 4, 6, 28).
4. *Semnopithecus* (figures 4, 6, 28).
5. Cat (postnatal; Latimer's unpublished data are withheld) (figures 8, 28).
6. Sheep (figures 5, 6, 9, 28).
7. Ox (figures 5, 6, 9, 28).
8. Pig (figures 5, 6, 9).
9. Horse.

Data not reproduced: Zuckerman and Fischer's (1937) macaques; Donaldson and Hatai's (1911) rats; Michaelis' (1906) and Wendt's (1909) postnatal humans. These tables are rather bulky, but they are quite accessible.

10. Prospectus of formulae, fetal and postinfantile, obtainable from all the data, reproduced or not.
11. Formulae for growth of brain weight/body weight after infancy.
12. Prenatal growth of brain weight/body weight.

4. Notes on the Data

Table 1. *Homo*. Fetal: Michaelis' fetal averages probably are too low in body weight for normal fetuses. Thus, at 9 months, he gives 1994 gm. A European infant weighs ½ again as much and even more at birth. The composite of three authors for the other human formulation seemed justified from a plotting.

Postnatal: Michaelis' and Wendt's data overlap excellently on plotting. It is uncertain how early one may initiate the series for a straight-line logarithmic formula. To be safe, nothing under the age of 4 years was used. This probably erred on the side of scrupulosity.

Table 3. *Orang*. Only male specimens from Anthony were used for formulae, because there is only one immature female, and adult sex dichotomy of size is very marked. Hrdlicka's are all mature specimens. They were not used, because their weight would have vitiated the calculation.

Table 4. *Semnopithecus*. The two species represented here are not far apart in their adult proportions. At any rate, one may doubt

that their growth behaviors differ too much to furnish a notion of growth in this genus.

Not tabled: *Rhesus*. Only data from beginning to recent completion of permanent tooth eruption were used for calculations.

TABLE 5. *Felis*. Anthony (1928) was checked against Ziehen (1901). The postinfantile straight line begins fairly with the 2-month age, regardless of the matter of dentition. (Correlation between onset of permanent tooth eruption and the straightening-out of the line of growth we are studying, is a problem for future investigators.)

Not tabled: *Mus*. Donaldson (1924) *computes* brain and body weights of Norways for every millimeter of body length, treating the sexes separately. The formulae he uses are Hatai's (1909):

$$Br = 0.569 \log (Bw - 8.7) + 0.554, \text{ when } 10 < Bw < 325$$
$$Br = 1.56 \log Bw - 0.87, \text{ when } 5 < Bw < 10.$$

Together,

$$Br = 0.825 \log \cdot (Bw - 4) + 0.233,$$

sexes combined; then a correction up and down is made for the sexes. These formulae are very completely empirical. They are hardly adapted for our purposes, however successful they may be for predicting brain weight from body weight.

I therefore reverted to Donaldson and Hatai (1911), for the form in which they presented the data upon which their formulae are based. That form is one of grouped data. I have disregarded the albinos, because I wished to avoid the complications from domestication wherever possible (for the artiodactyls, the data had to be from domesticated forms). For the straight-line formulae, only the data between body weights 15 and 485 gm., inclusive, were used.

TABLE 6. *Ovis*. Only the last three entries were used. They are considerably older than the first two, which, respectively, are fetuses and 1-month-olds.

TABLE 7. *Bos*. In the postnatals, only entries 3 through 7 were used. The first 2 entries are too young to fit the straight-line postinfantile formula, and entry 8 is the sole female among the immatures. Hence, the entries used represent a male growth curve only.

TABLE 8. *Sus*. The entries represent means of lustra. The period of prenatal growth so recorded is exceptionally long.

TABLE 9. *Equus*. On these principles, only the starred entries were used for formulation.

C. RELIABILITY OF THE FORMULAE

TABLES 11 and 12.

If even a small series happens to form a good straight line, it favors reliability. If the points of postinfantile growth are spaced over a considerable distance, they favor an accurate formula more than if they be bunched near one end of the putative line. A large population is generally more reliable than a small one, but I know of no satisfactory formula for calculating the P.E. of a line.

In the matter of sex difference, the human values of TABLE 11 are very close together; enough to raise the possibility that the difference is not significant. A collateral experiment on figures of E. Boyd (1942) (see below, under D1, *Man*) reverses the position of the sexes, in point of relative size of the constants. However, the brain-body ratios are never alike in the two sexes; this is known empirically. So, while they are known to be different in the sexes at various ages, we cannot be sure, from our formulae, which grows faster in the brain/body ratio, the male or the female.

The anthropoid ape data are meager, yet, together, they agree closely (TABLE 11).

Sex discrepancy in *Rhesus* (TABLE 11) probably exists, but the *size* of the discrepancy is at least striking.

For *Semnopithecus,* the data on the immature are few, the line is short, the few adults probably deflect the line. Perhaps a value of .14+ for the *b*-constant would be more nearly truthful. On the other hand, the sexes in *Rhesus* deviate considerably, and cephalization in the Cercopithecidae varies strongly. So, perhaps, the difference in growth-ratios also, between *Rhesus* and *Semnopithecus*, is real enough.

It would take but very few more fetuses, properly placed, to swing the fetal slope in alignment with the human (FIGURE 4).

The alignment of the postnatal cat data is fairly good. The prenatal data are peerless.

The rat data are excellent, so that the sex difference is probably genuine.

The materials for the postnatal Bovidae and the horse are not abundant, but the agreement among them (TABLE 11) is excellent. It points to *sub*equality, which is what one might look for. The prenatal pigs cover an exceptionally long period of growth. The entries represent averages of groups, and the number of samples is very unusual. But the data do not line up very well, although a straight-line general trend is acceptable. The point will be brought up again later.

D. BEHAVIOR OF THE GROWTH CURVES

1. Man

FIGURES 1–4, 6. TABLES 1, 11, 12.

The mass tendency of growth of brain and body weight in man and woman, from the earliest fetal stage available, describes a steep straight line when plotted logarithmically. At some indeterminate period, the line very gradually deviates from the straight. Birth occurs while the deviation is still too slight to be ordinarily perceptible. Thereafter, during infancy, the curvature becomes marked. More abrupt than the fetal deviation is its convergence upon, and merging into, another straight line, which characterizes growth, thenceforward. Just when this new straight line becomes valid, is also indeterminate; but, for practical purposes, it has safely supravened by age 4 years.

Since our fetal data have not warranted separating the sexes, the line we have drawn is a sex compromise. At best, it could hardly be expected to join perfectly the postnatal constellations of the sexes.

The rest of the procedure is graphed in FIGURE 3 (see TABLES 11 and 12) which gives velocities of growth for each sex, assuming the fetal velocity as about 1.0098.

Mathematically,

$$\frac{dY}{dX} = b,$$

whenever $Y = A + bX$. Let b' be fetal velocity, b'' postnatal velocity. Then:

$$♂ : b' - b'' = 1.0098 - .06326 = .96874$$
$$♀ : b' - b'' = 1.0098 - .07010 = .89399.$$

In FIGURE 3, the values of b' and b'' are asymptotes. The S-curve is a skew logistic, and its integral is the growth behavior transitional between fetal and the established postnatal. As far as I know, this integral is unsolved. However, fair values of Y' can be obtained from:

$$♂ : Y = \frac{.96874}{1 + \text{antilog}_{10}\,(1.6922X^3 - 18.3695X^2 + 67.6053X - 84.5844} + .06326$$

$$♀ : Y = \frac{.89399}{1 + \text{antilog}_{10}\,(-1.850X^3 + 17.980X^2 - 56.934X + 58.151} + .0701.$$

The essentials of our description are simply these, and they could have been immediately read out of the curves of FIGURES 1 and 2:

(1) The transitional period is marked by a velocity which is asymmetrically S-shaped;

(2) The adjustment to postinfantile growth rate, therefore, is much more abrupt than the deviation away from fetal behavior;

(3) For the data given, it differs quantitatively in the sexes.
But what lies back of this manifestation?
Donaldson (1917, p. 136) says:

"At birth cell division is still in progress, and this is true for both man and the rat; moreover, for some time after birth cell division continues—especially in the cerebellum. Allen (1912) finds in the *cerebrum* of the rat some cell division up to the twenty-fifth day of postnatal life, after which time it diminishes rapidly and soon becomes insignificant. In the cerebellum, however, postnatal cell division is more abundant than in the cerebrum and is responsible for considerable change. The enumerations are given in TABLE 3.

"TABLE 3

BRAIN OF ALBINO RAT. MITOSES IN ONE CUBIC MILLIMETER OF NERVE TISSUE (ALLEN, 1912)

Age days	No. of mitoses—Brain	
	Cerebellum	Cerebrum
1	1597	430
4	2111	447
6	....	193
7	4848	...
12	839	37
20	127	23
25	00	27"

Whether coincidentally, or whether in terms of cause and effect, the cessation of neural mitoses, apparently variable locally, occurs during the transitional period. The steep fetal velocity covers a period of growth in weight, plus number of cells in the brain; the gentle postinfantile velocity covers a period of growth in size of cells, without increase in number. However, much of the rest of the body continues, in the latter period, to increase in terms of both cell multiplication and cell size.

A glance at FIGURES 5–9 will indicate that man is not peculiar in these matters.

2. Man and Other Primates

FIGURE 4. TABLES 1–4, 11, 12.

At face value, the human fetal slope is the steepest; the postinfantile, one of the gentlest. In the matter of the fetus, the monkey data are too few for a positive conclusion. (See also below, under "Cats.")

On the postinfantile side, the story is clear: Monkey brains grow at the *steeper* rate; man and anthropoid stand off together with *lower* rates. In fact, the anthropoids have a lower rate than man. Consequently, the rate does not correlate perfectly with relative brain weight.

Moreover, the fetal rate (*i.e.*, over the distance for which we have data) does not account for the great preponderance of the human brain weight and the "second-prize" weight of the anthropoid. For the human and *Semnopithecus*, rates are *subequal*, anyway, and the two chimpanzee entries are consistent with the scheme. Thus, an average between the human formula from Michaelis and that from the composite series (TABLE 12) is $Y = -.7345 + .9619X$. If this, in turn, be averaged in with *Semnopithecus*, we have a rough general trend of $Y = -.64575 + .8847X$. The two chimpanzee entries are joined by a line which happens to parallel it exactly. A slope of something in the neighborhood of .9 should be a fair center of approximation for Primates. It is very close, we see, to 1.0; —tan 45°, where increase in brain logarithm would exactly pace increase in body logarithm.

While the rate may be one factor, then, if human (and chimpanzee) rates are at all higher than monkey, it must be less important than some other. Notice that, at equal body weights, the human brain is heavier than the simian; a larger percentage of the human body is brain when total body weights of the fetus are equal. This ascendancy had to be achieved at some age earlier than those registered on the chart. Further than this, at a given body weight equal in man and monkey, the monkey is the closer to birth. When the monkey is being born, thereafter to enter upon the transitional deviation that leads to the side-line position of the adult, the human, still underdeveloped by comparison, is continuing to travel up the fetal curve. The achievement of the human *proportion, as well as size,* of brain *demands an enlarged body.* It looks as though the human, to achieve his high cephalization, shifted the mutual relationship between two blocks: the energy of growth which determines size, and the urge toward definition which determines morphological maturation.

In Section IV, we shall see that the requisite of an enlarged body, as a *sine qua non* of a proportionately larger brain, is borne out by phylogenetic considerations.

The postinfantile ape behavior will no doubt raise anew the question of whether the difference between the stated human growth rate and the anthropoid is genuine or spurious. It says that, although the monkey brain, after infancy, grows at a *higher* rate per body than the human, the human grows at a higher rate than anthropoid.

It is true that the human data all represent natural deaths, but so, for that matter, must at least a goodly share of the anthropoid. Presumably, the bodies were more or less underweight. Then the body weights would be too low per brain weights. Would the underweight condition be so distributed along the entire line as to alter, or not to alter, its slope? I do not know. For the sake of discussion, let us assume, first, that the human line should more nearly approximate the anthropoid, or even be lower. As an experiment, then, I plotted the brain weights in E. Boyd's (1942) Table 27 against her body weights in Table 8 (Minneapolis and Chicago children). Of course, the brains did not belong to these children. At least, this should correct for body weight deficiency, though not for brain weight deficiency (which probably is less discrepant), and we might look for a lower slope, after the doubt just raised concerning the condition in man. Here are the results:

$$♂ : Y = 2.8215 + .06859X \qquad y = 663.0x^{.06859}$$
$$♀ : Y = 2.8701 + .05002X \qquad y = 741.4x^{.05002}.$$

This reverses the sex behavior of the slopes, as compared with the formulae of TABLE 11; still, the male formulae are practically identical. At any rate, the new slopes differ remarkably little from the old. The behavior, therefore, seems genuine. Then let us reverse the assumption. Should not the ape slope be much steeper—intermediate between man and monkey? In answer, chimpanzee and orang behave almost identically. Thus, their data become reliable, in spite of their paucity.

Nevertheless, it is obvious from the chart that the several brain-body positions of man, ape, and monkey can be achieved without demanding the straitjacket of an *a priori* consistency. What we are witnessing, after mitosis has ceased, is increase in brain weight divorced from the additional factor of cell multiplication. Not being a neurologist, I prefer to waive further comments on this phenomenon. It is enough that we have seen that brain preponderance is a function of the fetus. However, it must be that the possible factor of steeper increase in brain with respect to body is practically over with by the time our measurable period begins; for thereafter, another factor is manifest: brain preponderance is in terms of a steeper increase in *brain-plus-body-weight per level of morphological maturation.*

3. Man, Other Primates, and Some Ungulates

FIGURES 5, 6. TABLES 6–9, 11, 12.

a. As compared with the primates, the cattle show:

(1) A gentler fetal slope (average for the three together: .7801, as compared with the primate, .8848).

(2) Postinfantile slopes on a par with those of the monkeys, but steeper than those of man and the apes.

(3) About the same range of fetal slopes as that from monkey to man. If, in TABLE 12, we subtract one b-value from another, we obtain:

Cattle:	
Sus-Ovis	.1372
Sus-Bos	.2562
Ovis-Bos	.119
Homo-Semnopithecus:	
Using the composite human formula:	.2015
Using Michaelis' data:	.1065
Using the mean of these two:	.1540

But this may signify very little.

(4) A marked equality or subequality in the magnitude of the postinfantile slope; whereas the Primates vary, from monkey to anthropoid. This should be noted in conjunction with the taxonomic ranges represented, which are, respectively, Hominidae, Anthropoidea, Cercopithecidae, and Suidae, Bovidae among artiodactyls, and, in addition, two of the Equidae.

(5) What hardly appears from the chart, yet is necessarily of a piece with the rest of the traits, is that the range of *cephalization* among these ungulates is very narrow; it is very wide among the primates.

Cephalization is a term to be exploited in the section on phylogeny. Just now, it is convenient to define it as:

$$\text{Cephalization} = k = \frac{(\text{Brain weight})}{(\text{Body weight})^{.56}}$$

The values for our ungulates and primates are:

Equus	.43	
Bos	.30	
Ovis	.32	
Sus	.17	
Range:		.26
Cercopithecidae (without baboons)	1.11	
Simia	1.21— .75	
Homo	2.75	
Range:		1.64—2.00

The situation reduces to this:

Primates. Man and monkey have subequal fetal slopes. Man climbs that slope (using the earliest periods registered on the chart, and disregarding the unknown situation anterior to them) along a slightly higher elevation (per body weight). More notably, he climbs it much farther before turning aside to the right. After he turns, he travels but a short distance, and on a much more gradual rise than the monkey. As a result, he is bigger-bodied, bigger-brained, more highly cephalized.

Artiodactyls. Cattle have subequal fetal slopes; these slopes are slightly more gradual than the Primate; no one of them climbs along a markedly higher level (per same body weight) than another. *Bos* climbs this slope farther than *Ovis* or *Sus,* before turning aside to the right. After turning, all three travel on a rise of the same general magnitude as that of *Rhesus* or, for that matter, of *Felis.* (See TABLE 11.) Result: *Bos* is bigger-bodied, bigger-brained, but no more highly cephalized than *Ovis; Ovis* is smaller bodied, slightly bigger-brained, and, along with *Bos,* a little more cephalized than *Sus.*

That it takes a number of metric factors to bring on the end-product called an adult, should be clear; also, that these factors can vary in a number of combinations; but further, that the variety is not random, for the combination has taxonomic value. Shortly, we shall be exploiting those devices of Dubois, the relational exponent and the cephalization coefficient. They have been useful for several decades, and the criticisms of their shortcomings (which are real) have not destroyed them. But if we expect to use them, it is very advisable to go behind the scenes before these actors take the stage.

b. What then, is the summary of factors by which the mean adult reaches his final position on the chart?

(1) The initial position of his fetal slope;
(2) The degree of that slope;
(3) The level at which he leaves that slope and turns to the right;
(4) The length of the transitional curve;
(5) The curvature of that curve;
(6) The degree of the postinfantile rectilinear slope;
(7) The distance traveled along that slope.

Factors 2 and 6, taken together, form an angle which is smaller, the greater the stepdown in velocity from the fetal level to the postinfantile. The anthropoids and man have the smallest angle; in fact, the anthropoid drop in velocity is even greater than in man. Yet, the anthropoid is only a "second-prize" brain. So this compound factor must be taken in conjunction with another: the level at which the postnatal line "peels off" to turn to the right. As a practical measure, it is best indicated by taking the point at which the projected fetal straight line would intersect the projected postinfantile. This may be achieved by solving the two formulae as a pair of simultaneous equations. In short, the location of any total one of the developmental lines may be viewed as essentially a pair of straight lines forming an angle at some point in a Cartesian field and in terms of three quantities: the velocity or slope of *either one* of the two straight lines; the point X, Y where the two intersect; and the difference between the fetal and the postinfantile velocities. This leaves the beginning of the fetal line indeterminate, but, for present purposes, inessential. The mean point of adulthood still remains to be determined, and this is essential.

4. Cats and the Law of Allometry

We broaden the comparison by considering FIGURE 8. No fetal formula appears in TABLE 12, simply because Latimer's data really are *too* good. Now we can see definitely a case of something suspected hitherto: the fetal line is not really rectilinear at all (at least it is obvious in the cat), but considerably more complex. The total cat path, from its earliest record to a projected merging with the postinfantile period (and perhaps even that should be included), may be a parabola of no less than third degree. It gets steeper, as it approaches birth, and a point of inflection in the line is suggested at that period. There may, also, be one near the lower or earliest end of the constellation.

If the other two long fetal lines that we have (Michaelis' human averages, and the pig) be scrutinized closely, a similar possibility will appear, though it is less pronounced. Being less pronounced, it takes a rectilinear fit fairly well. So, as we have been comparing slopes of Bovidae and Primates, we have overlooked the possibility that we should do so only with those portions of the line that are strictly comparable. But what is the unit by which they could be compared?

It should be that of logarithmic cycles. Thus, data on the brain of the fetal pig are given for a little over three logarithm cycles; the cat's covers about 2½ cycles; Michaelis' human averages, a little less than 2 cycles. Viewing these lines as curves having at least one arc, the deepest place in the arc occurs at about the onset of the last prenatal logarithmic cycle. That region is very clear in the cat; it is fairly so in Michaelis' humans; the pig is less certain. If the lines are really curvilinear, it is readily understandable not only why, within an order, the pieces of slope have varied as much as they have, but also why the values of the A-constant differ so widely.

Since, today, there is a widespread tendency to apply the "law of allometry" ($y = ax^b$) to all sorts of growth behavior, it is timely to caution that the law often may be but a first approximation, pending the more accurate application of complex exponents in place of the b in $y = ax^b$. If the "law of allometry" be adopted too wholeheartedly, it can turn obscurantist. For, if undulations actually be present in a line of growth through which we have run a rectilinear shortcut (and "shortcut" is exactly what it would be, if the variable y keeps changing its rate of increase, with respect to that of x, by first accelerating, then decelerating), they are real phenomena which that formula screens from further investigation. If our fetal growths have been really undulatory, all the time, then we have been comparing pieces of arc without first standardizing their lengths. This does not mean we have been wasting effort: an undulatory set of growth curves would still have to be analyzed along the lines laid down here.

These reservations could be easily illustrated, if necessary, by way of the artiodactyls, but lack of space prevents this. Considered this way, the apparent failure of the fetal and postnatal lines of human ontogeny to join perfectly (FIGURES 1 and 2) may not be due entirely to individualisms of technique in the collectors (although some of both the fetal and postnatal data are Michaelis', which is one reason for using his material), but may reflect, also, a genuine condition, one resembling the feline.

SECTION III. COMPARATIVE ANATOMY

Part One

RANGE OF MATERIALS: ADULTS

1. Index of Data

1. *Ungulates.* Brummelkamp's (1939c) Table I. See table 13.
2. *Rodents.* Brummelkamp's (1939b) Table I. See table 14.
3. *Carnivores.* Crile and Quiring (1940); Hrdlicka (1905).
4. *Primates.* Spitzka (1903), averages for the species mine; Hrdlicka (1925), his averages corrected. *Homo:* Crile and Quiring (1940). (My average from all adults.)
5. *Other Orders.* Crile and Quiring (1940); Hrdlicka (1905).
6. *Palaeanthropoi.* Hrdlicka (1930), his own data and others'.
7. *Reptiles.* A: Crile and Quiring (1940); B: Dubois (1913).
8. *Amphibia.* Brummelkamp's (1939d) Table I, from Dubois (1913) and Donaldson (1910).
9. *Weights of Human Brain by Parts.* Marshall (1892).

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Table

13. Brain and body weights and cephalization coefficients of Ungulata. Figures 13, 18, 19, 20, 22, 28.
14. Brain and body weights and cephalization coefficients of Rodentia. Figures 14, 20.
15. Brain and body weights of Carnivora. Figures 16, 17, 20, 22, 28.
16. Brain and body weights of Primates. Figures 15, 20, 22, 28.
17. Brain and body weights of Edentata, Pinnipedia, Chiroptera, Insectivora, Cetacea. Figures 20, 21.
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25. Mammalian genera in 11 lustra by log body weight. FIGURES 20, 21.
26. Twenty-three exponents of cephalization. FIGURE 22.
27. Exponents of cephalization $Y' = a' + b'X' - c'X'^2$, where the origin of the coordinate axes is taken at $X = .2385$, $Y = -1.6217$.
28. Calculated Y for *Homo* line, compared, from the formulae of TABLES 26 and 27.
29. RY for six formulae of TABLE 27.
30. Values of X where the differences between mammalian Y and that of a reptile of equal X is a maximum, by orders.
31. Values of l, where $l = \lambda(\text{mammal}) / \lambda(\text{reptile})$, λ being the slope of any parabola in TABLE 27.

PART TWO

PRELIMINARY

a. Hitherto, as described in the Introduction, we have presupposed that a line of mean tendency in growth was a sort of summary description of the path actually traveled by the average, or standardized, individual as he grew. That it is an assumption, should be emphasized now, for the last time. As a practical matter, the measurements on fetuses have been taken at one moment of growth in each individual. This cannot be simply assumed to be the same thing as measuring the same individuals over a successive period of time.

We propose now to compare the adults of extant genera, and to do so by orders. We ask, Do the members of an order group themselves in such a way as to give a definite and consistent scheme?

This is an appeal to comparative anatomy. It would be very desirable to be in a position to pass from these modern animals to their phylogenetic antecedents. Some day, this will be possible; at this juncture, it is not. All that we can say is this: If it should prove that modern members of a common order plot in a regular fashion that is even mathematically formulable, we can be morally confident that the order itself has differentiated in no haphazard way.

Technically, then, we shall seek to formulate curves, as before; and, since such curves can represent only connections between extant contemporaries, let us call them, for want of something better, "*comparative anatomy*" curves. The true phylogenetic curve would connect a series of direct evolutionary ancestors. It would lead up through a succession of fossils, located in the time of previous geological epochs, to present times and extant forms. If, for a moment, we glance at almost any of the graphs that follow, we may picture the surface of our sheet as located in the time of today, lying on an indefinite pile of such sheets, each charting the condition of the animals extant in some previous epoch. The true phylogenetic line should wander *up* through these sheets, piercing each in turn, until it emerges on the surface now exposed to us.

Immediately, it will be seen that time is the third dimension, its axis being at a right angle with the plane of the paper we are looking at. The true phylogenetic curve, in other words, is one of three coordinates, x, y, z, in which x and y remain the measures, respectively, of body and of brain weight (taken as logarithms X and Y), while z is a time-scale.

Suppose, next, we imagine all our sheets to be transparent. Then (confining our example to the primates), on the top sheet we may perhaps draw a curve connecting the modern primates with each other: the comparative anatomy curve. Gazing straight down through our pile, now, we see true phylogenetic curves coming up at us. How closely, however, does our pseudo-phylogenetic curve appear to cover, or project its shadow upon, the true phylogenetic line? More technically, how closely does our comparative anatomy line coincide with the projection of the true line onto the x, y plane?

This is what we cannot answer, as yet, for want of sufficient fossils. This is why we must content ourselves with plotting the curve that lies on our top sheet alone. This means tracing curves on the basis of comparative anatomy. At least the principles to be laid down anticipatorily should then need merely to be expanded into the geometry of three dimensions, whenever the fossil record becomes adequate.

b. The comparative-anatomic path actually has been treated by some authors as though it were the true phylogenetic path, particularly since Dubois introduced the view that the brain weight of any mammal (eventually, of any vertebrate) is related to its body weight by a formula $y = ax^b$ (1897). (Dubois used a different set of symbols. See below.) He has been followed and supported by Lapicque, Anthony, Ariens-Kappers, Brummelkamp, and others (see Bibliography).

The mathematical law, $y = ax^b$, has found widespread use in other biological investigations, under the name of "law of allometry," especially since the impetus given it by J. Huxley (*Problems of Relative Growth,* 1932; see the bibliography in Hersh, 1941). In the literature on brain/body-weight, it has been variously written $E = kP^r$, $E = cP^r$, $E = kS^r$, etc., so that, in the following development, any or every one of these forms will have to be used, depending upon which author we are discussing.

A. THE "PHYLOGENY" OF BRAIN/BODY WEIGHT EXPRESSED AS $y = ax^b$

1. The Relational ("Interspecific" or "Phylogenetic") Exponent and the "Cephalization Coefficient"

In 1897, Dubois, assuming that certain animals, closely related, but differing widely in body size, must have equal cerebral organization, propounded that their brain weights would be to each other as the rth power of their body weights:

$$E : e = P^r : p^r \quad \ldots\ldots\ldots\ldots\ldots \quad (1)$$

where E and e are weight of "*encephalon,*" P and p are body weight, the capitals represent the bigger animal of a comparable pair, and the minuscules the smaller animal. Dubois initially compared the following animals:

Simia satyrus — *Hylobates syndactylus*
Simia satyrus — *Hylobates leuciscus*
Oryx beisa — *Cephalophus maxwelli*
Felis concolor — *Felis domestica*
Felis leo — *Felis domestica*
Mus decumanus — *Mus musculus*
Sciurus bicolor — *Sciurus vulgaris*

E, e and P, p being measured and therefore known, r can be found:

$$r = \frac{\log E - \log e}{\log P - \log p} \quad \ldots\ldots\ldots\ldots \quad (2)$$

In every case tested, the values of r *approximated* .56. Even with many further pairings, including all or most classes of vertebrates, the quantity generally varied within what seemed to the investigators a reasonably narrow range. Hence, r, which, when we write $y = ax^b$, is b, has been termed the *"relational exponent."* (See Dubois, in Bibliography.)

Once $r = .56$ is taken as universally valid, the brain weight, y, of any animal is related to its body weight, x, as:

$$E = kP^r \text{ or}$$
$$y = ax^b,$$

where $r = b = .56$. In this formula, if y and x have been measured, a can be calculated:

$$a = \frac{y}{x^b},$$

and a (or k, above) is the "coefficient of cephalization." If, for instance, we have two animals of practically identical body size (say gorilla and lion), but obviously of discrepant brain size, then the values of a will differ, because their y differs; and the size of a favors the gorilla, who is more "cephalized." Conversely, then, if a has been ascertained for various kinds of animals, and the weight x of an animal be known, $y = ax^{.56}$ gives approximately the brain weight. Where two animals are equally cephalized, but differ in brain and body weights (*e.g.*, lion and cat), they will actually be related (reverting now to the Dubois symbols) as:

$$E : e = k\,P^{.56} : k\,p^{.56} \quad \ldots\ldots\ldots\ldots \quad (3)$$

but k being identical for both, the formula reduces to EQUATION 1.

At the present date, those individuals who are satisfied that intelligence is not a correlate of brain mass, will discredit the coefficient completely. On the other hand, those who are not ready to go so far and who believe that mass is still one correlate, even if only an imperfect one, of cerebral capacity (whatever be the definition of that term), will insist that the relative size of brain in gorilla and lion is not purely coincidental or insignificant. At least, the presuppositions underlying the work of Dubois and his followers, at the close of the last century, are no longer tenable. At that time, it was hoped that an anatomical separation might be effected between the "psychic" brain and the "somatic"; the former controlling the "higher" mental functions, the latter, the physiological ones. Von Bonin, in fact, apparently rejects the Dubois scheme, primarily because of this naïve conception (1937). Criticisms, however, must lie in abeyance until after we have examined the scheme more fully.

The formula $y = ax^b$ is grasped better if it be pictured. On a log-log scale, it turns into $Y = A + bX$, where $Y = \log_{10}y$, $A = \log_{10}a$, $X = \log_{10}x$. Thereby, b becomes the slope of a straight line, and A is the value of Y, when $X = 0$. In such a disposition, the pairs of animals of Dubois should be united *intra se* by sloping, parallel bars which, when projected to the Y axis, should mark values of A (FIGURES 10, 11, 13, 14).

2. The Ontogenetic Exponent

One might be led to expect that, if cats and tigers are related as

$$E : e = P^{.56} : p^{.56},$$

then different-sized domestic dogs would most certainly be so related. Certainly they are in the main equally "cephalized." But no; they are related as

$$E : e = P^{.25} : p^{.25},$$

.25 being an average figure obtained from numerous pairings as before. This finding is Lapicque's (1898, 1907, 1908, 1912). The constant $r = .25$ has been termed the "ontogenetic" or "intraspecific" exponent.

Why animals within a species should so behave, has led to speculations (*e.g.*, Dubois 1923). Whatever the explanation, the Dubois school has built further upon it. One may see its use by Anthony (1928), who extensively compares animal brain weights; or Harris' experimental use of it (1929); also Ariens-Kappers (1929, 1936). Anthony and Coupin (1925, 1925–26, 1929) have erected out of it an "Index of Cerebral Value," which shall be discussed a little further on.

3. Discussion of the Dubois System

The rationale of the exponent or slope .56, to my knowledge, has never been explained. That all the vertebrates compared by Dubois and his followers give values that seem to them satisfactorily close in agreement, has naturally led them to conclude that there is something fundamental in, and common to, all the vertebrates, which is masked by this number.

However, the diverse values of the cephalization coefficients have led to other speculations.

At the outset, Dubois' comparisons of animals having different values of y, x, and a are not strictly and explicitly phylogenetic. A cat and a lion are two modern Felidae. Their mathematical relationship is one existing today. The one animal is not derived from the other. They have had a common ancestor which, whatever else may have been true of it, could not have equaled both of them in body and brain size. The fact that both have the same cephalization coefficient may be explained as one will. Either it was the possession of their common ancestor, or else both lion and cat have arrived at the same value by a parallelism. If the former be the case, then the bodily differentiation in point of size has proceeded without any change in cephalization, and we have in the cephalization a now static situation. If the other be the case, then cephalization has been an identical and concurrent achievement, even while brain and body size were differentiating. This would lead to the conclusion that there has been an identical potential towards cephalization which inhered in the common ancestor.

These are the speculations which must suggest themselves to the student who is so evolutionally-minded as to insist upon raising to the surface the implications of the Dubois system. The Dubois school has recognized that there must be implications, although it has not expressed them in such forms as above. Instead, Dubois and his followers have sought to explain the differences in the cephalization coefficients in terms of quantitative cytoarchitectonics. The most recent studies are those of Brummelkamp (1939–40; see also Dubois, 1913). He devises a scale for the cephalization coefficient (which he writes as c), such that:

$$c = \sqrt{2}^{a} \text{ or } \log c = a \log \sqrt{2}, \qquad \text{where } a = 0, 1, 2, 3 \ \ . \ \ . \ \ .$$

(See our FIGURES 13, 14.) Basing his theory upon Dubois (1913 *et seq.*), he rationalizes this in terms of cytoarchitectonics. However, into this aspect of the question we shall not delve. The points that are relevant here are:

(1) Brummelkamp makes evolutionary implications practically inevitable, by concluding that, within any order of animals (*e.g.*, rodents or ungulates), cephalization increases saltatorily in units of $\sqrt{2}^{a}$, as one passes from the less cephalized of the order to the more cephalized.

(2) Brummelkamp's own graphs indicate that greater cephalization accompanies increased body size. An aspect of the phenomenon that is crucial to the development of the system to be elaborated in the present essay, but which is *not* explicit and unalienable in the Brummelkamp system, is the possibility that the different stages of body size, plus their relative amounts of brain, as illustrated in FIGURES 13 and 14, correspond, in general, to the path actually taken by the order in its quantitative cerebral development. This, then, is the issue: Can animals within a given order, having small bodies and a "lower cephalization," be considered at all as "contemporary ancestors"? To this we must return later on. Meanwhile, now that the character of the system of the Dubois school is before us, we may turn to some critical analysis.

4. Criticism of the Dubois System, and of Some Derivatives from It

a. The fact that the scheme is built on a naïve philosophy of the brain has already been mentioned. This, none the less, would not overthrow a set of empirical findings. If the Dubois and Lapicque equations really hold, then they are empirically valid, however they may be explained. But do they hold?

b. The method of ascertaining values of r or of k was one of simple algebra, and one of pairing together animals assumed to have equal "psychic" endowments. This would not be considered good statistical technique today. Then, can one reach the same results by using modern methods? As will develop, one can do so only within certain limits which exclude many contradicting cases, notoriously among the Primates. In fact, it will transpire that Dubois' obtaining $r = .56$ out of comparisons between orangs and gibbons was only a fortunate accident, and one, furthermore, that is its own refutation. No cerebral anatomist would consider the brains of gibbon and orang at all comparable in the sense of *Felis leo* and *Felis domestica* or of the two *Mures* or *Sciuri*.

c. This weakness is critical, not only in the matter of $r = .56$, but in that of $r = .25$. A closer examination of Lapicque's use of his dog material throws an additional doubt upon the scheme.

Lapicque grouped his animals into ten body sizes and weighed brains and bodies. Then, by comparing group I with group II, II with III, etc., he obtained a mean r of approximately .25.

The question now arises: What about man? Should not the relation between male and female run according to $r = .25$, assuming that they are equally intelligent, members of the same species, and different in body size?

Lapicque was writing in the early part of the twentieth century (1907) when the "emancipation of women" demanded from the highest court of appeal (that of the scientist) a clear proof that women were men's "intellectual equals." Lapicque evidently believed he had supplied it. However, we do not mean to imply that he produced his proof on a direct and explicit demand. Here are Lapicque's operations:

$$\begin{aligned}
♂ : P^r &= 60\,000^{.56} \text{ gm.} = 498 \\
E &= 1\,360 \text{ gm.} \\
k &= 1\,360 \div 498 = \mathit{2.73} \\
♀ : P^r &= 54\,000^{.56} \text{ gm.} = 448 \\
E &= 1\,220 \text{ gm.} \\
k &= 1\,220 \div 448 = \mathit{2.72}
\end{aligned}$$

From the values of k, he concludes, *"Il y a égalité."*

Probably the most striking trait of this arithmetic is the use of $r = .56$, instead of $r = .25$. Lapicque insisted that men and women were so unlike, somatotypically, as to make the difference one of generic rank. Whether this difference is more marked than those between a mastiff, a greyhound, a dachshund, and a pekinese, he does not say. Anyway, were we to use Lapicque's own values of P and E, and the exponent $r = .25$, we should obtain:

$$\text{♂}\ k = 8.48$$
$$\text{♀}\ k = 8.02$$

Voilà qu'il n'y a pas d' égalité.

We confess a surmise that it was the failure to obtain equality here that led to Lapicque's use of $r = .56$. But if we fall in step with him and use the data from Welcker's (1903) 4 executed males and 3 females, we obtain:

$$\text{♂}\ k = \frac{1461}{59270^{.56}} = \mathit{3.13}$$
$$\text{♀}\ k = \frac{1249}{50800^{.56}} = \mathit{2.89}$$

From Crile and Quiring's (1940) 32 males and 9 females, of assorted races, we obtain:

$$\text{♂}\ k = \frac{1350}{65544^{.56}} = \mathit{2.70}$$
$$\text{♀}\ k = \frac{1214}{49755^{.56}} = \mathit{2.86}$$

It seems, therefore, that Lapicque struck his "*égalité*" by accident. If, on the other hand, we stop assuming $r = .56$ and by a modern method seek the empirical equation for the human situation from the raw data of both sexes, we obtain,

From Lapicque's figures: $Y = .5255 + .541X$
$y = 3.35x^{.541}$
From Welcker's: $Y = -2.4053 + 1.167X$
$y = .03933x^{1.167}$
From Crile and Quiring's: $Y = 1.2773 + .385X$
$y = 18.94x^{.385}$

The discrepancies speak for themselves.

Returning to Lapicque's dogs and his intraspecific exponent, FIGURE 12 should illustrate the reason why his r is so much less than .56. The adult dogs, each presupposing an ontogenetic line such as that already developed in Section III, align themselves definitively so that the axis of their adult scatter inclines at a slope of .23 (using Lapicque's own data, and solving by the method of weighted-averages). Morphologically interpreted, small domesticated dogs have unduly large brains, and *vice versa,* when a slope of .56 is used as a standard of reference. If we had the individual measurements, we could find a correlation coefficient by modern statistical methods, and we might find that man's selective breeding which has sorted dogs into sizes and strains, has "infantilized" or dwarfed some and has "feralized" others, or increased their body size without correspondingly pushing up their brain size. This would be a case of "stretching" the species along the X-axis of a graph, without distorting in equal proportion the Y-axis, a phenomenon which is handled in analytical geometry under the term "transformation of axes." (This concept will prove very useful later on.) Unfortunately, we do not have the requisite data on wild Canidae to verify this by way of a proper, and a very interesting, comparison.

And if man were to transfer the breeding and domestication to cats and tigers, he might well find "ontogenetic" slopes in each. Yet, the *dead center* of the cat population might still connect with that of the tigers by way of a slope of .56.

d. The next criticism concerns the "Index of Cerebral Value" developed by Anthony and Coupin (1925–26, 1929).

This time, the topic is one of ontogeny. The object is to measure the brain of the immature in terms of its proportion to that of a definitive adult.

Let the adult brain weight $PE = kPS^r$, where $PE =$ "*poids encéphalique,*" $PS =$ "*poids somatique,*" $r = .25$. Let PS' be body weight at some immature stage. Calculate $k\,PS'^r = PE'$. Let PE' and PS' be known empirically. Then, $\frac{PE}{PE'} = \frac{k\,PS^r}{k\,PS'^r}$, which fraction is the "Index of Cerebral Value." In a 5-months-old fetus, it is far < 1; at about age 7 years, it is a maximum (> 1); by age 30 years, it drops back to 1.

If, on FIGURE 1 or 2, we were to draw a straight line of slope .25 (*i.e.,* 14°–15°) through a mean adult value, the reason for this rise and fall would be clear: such a line would cut the curve of FIGURES 1 or 2 twice.

In all justice to these authors, they admit that their device is a "stratagem." At the same time, it seems to me to carry the interpretation of figures too far when the fact that, after age 30, their index falls more in men than in women, and is coupled with their observation, "*ce que l'on* sait (italics mine): *la femme semble conserver mieux que l'homme pendant le période de décrépitude, l'intégrité de ses fonctions intellectuelles.*" By their own figures, the Index reaches the highest point in 7-year-old girls. Hence, it would seem to follow that the

7-year-old girl should be the culmination of man's intellectual development.

It must occur to the reader that the occasional use of $r = .25$ for one kind of comparison within the human species and that of $r = .56$ for another, even though the authors are not the same, leaves us wondering about the logic in the whole system. It seems opportunistic, when choice of one or the other depends ahead of time upon the results one desires. Harris (1929) has experimented with the device of Anthony and Coupin; but whether the device has enough substance to be a safe foundation for anything, may be left to the judgment of the reader.

e. The fifth criticism applies to the developments of the Dubois system by our Dutch contemporaries.

I have reproduced Brummelkamp's data for ungulates and rodents (TABLES 13, 14), both to make the present criticism clearer and also because the data will be useful later on.

FIGURES 13 and 14 show the scale made up of a set of lines sloping at $r = .56$, with the vertical distances between them equal, as already explained. The rise in cephalization thereby is indicated as saltatory. But is the sloping scale convincing?

(1) The vertical distances are so small that "the farther 'tis from England the nearer 'tis to France." Some of the points—in fact, all of them—are data from very small populations; the probable errors must be large. A fundamental of Dubois' exponent is that species within a genus must be equally cephalized. However, here the genera *Mus, Arvicola, Cervus* are indicated as having more than one cephalization. This renders suspect those genera represented by only one species.

(2) What virtue is there in averaging all specimens that apparently cluster about any single diagonal, when they follow no taxonomic scheme? If this can be done within an order, why could it not also be done where two orders overlap? What do you have after doing so?

(3) In fact, had the sloping scale not been superimposed, we should have seen a scatter-field with a curved axis of orientation. This is an important matter, which Brummelkamp has not exploited. It is cardinal to our exposition later on.

f. There are certain further criticisms to be had from von Bonin, who expresses some of the foregoing as well. But, as he follows up his objections with a constructive analysis of his own, it would be simpler to state his entire position at one time. This we now do.

B. VON BONIN'S CORRELATION COEFFICIENT AND REGRESSION FORMULA FOR THE MAMMALS AS A CLASS

1. Description

Von Bonin (1937) reviews in part the history of the problem of brain/body weight relationship, from Manouvrier and Snell to Dubois; then he says (*Ibid.* p. 380): "While Manouvrier's work shows all the care and critical self-control that are the signs of a great mind, Snell's and Dubois' work had laid itself open to criticism on several points. First, we have no right to introduce such conceptions as psychencephalon and somatencephalon as measurable quantities. Secondly, it is tacitly assumed that higher intelligence is due to (or associated with) greater brain weight or greater weight of the psychencephalon, and the cephalization coefficient is then taken as a measure of intelligence. But nobody has ever satisfactorily defined intelligence in such a way as to include animals, and, moreover, we know the behavior of only a very few animals with some degree of accuracy. To suppose, therefore, as Dubois does, that each one of certain pairs of mammals has the same intelligence as the other one, is merely begging the question. Clearly, we shall have to avoid all references to intelligence and all preconceived hypotheses about the relations of mind to the brain and define our task thus: to find out whether there is any law regarding the relation between body-weight and brain-weight expressible in numerical terms."

Von Bonin considers that the piecemeal pairing of animals, in Dubois' manner, is not the right approach. Instead, he tackles the problem immediately at the class level. He sees the mammals first in the aggregate; a chart of all species (after the fashion of our FIGURE 21) is to him a correlation scatter-diagram. He asks whether there is a constant correlation over the entire range of the mammals, which can be expressed by a single coefficient. This would demand a straight-line axis. Von Bonin tests the rectilinearity thus: The correlation ratio $\eta = .9449$. By Blakeman's test, $\xi = .196 \pm .053$; and by R. A. Fisher's, $N(\eta^2 - r^2) = 22.56$ for 18 areas, "which leads to $P > .10$ for the probability of the correlation being linear." Thus, he calculates the correlation coefficient: $r = +.83459$, which is high, though not perfect, as one would expect. Hence, his regression formula for $E = KS^r$:

$$\log E = .655 \log S - .75 \pm .312/N,$$
$$E = .18\ S^{.655}$$

(where S = body weight, E = brain weight). This exponent, .655, is nearer to Snell's of 2/3 (= .666) than it is to that of Dubois.

He concludes (p. 388): "Former attempts to analyze the relation between body weight and brain weight suffer from 3 deficits: (1) they presuppose a correlation between intelligence and brain-weight, (2) they make suppositions about the intelligence of animals which are unproven, and (3) they are based on a conception of cortical functions which can no longer be considered valid. The attempt has here been made to work out the correlation between brain-and-body weight, using the same formula ($E = kS^r$) of relative growth as former authors, but taking into account the complete mass of data at present available. There is a close correlation between the logarithms of brain-and-body weight, and this correlation is linear. Brain weight increases as the 0.655th power of body weight. The value of the cephalization coefficient K differs from species to species. Whether or not this is an indication of the intelligence of animals must be left to the psychologist to answer."

Von Bonin does not examine piecemeal any taxonomic divisions within the class Mammalia. Hence, such schemes as those of Brummelkamp (see our FIGURES 13, 14) have no counterpart. He eliminates the possibility of any evolutionary interpretation, in the sense of Brummelkamp, or from the standpoint that, within a given order, the smaller-bodied animals with the lower cephalization coefficients can reflect a stage in weight-proportions once passed through by the larger-bodied, more highly "cephalized." Through the entire mammalian constellation of FIGURE 21, he passes a straight-line axis of slope .66. Then, for any given animal species, $y = ax^{.66}$. If x and y be known, a can be calculated; if x and a are known, y can be calculated. Von Bonin calculates a for 115 species of animals. In this situation, a becomes merely an auxiliary for ascertaining y from x; but it is unfettered with any of the rationale which the Dubois school attempted to lay upon it. Thus, von Bonin is antipodal to the Dubois school in his use of modern statistical technique; also in his assumptions, and the point from which to launch an attack upon the problem. His objections to Dubois, I think, are well taken. On the other hand, whether his remedy is equally good, is a matter worth examining.

2. Criticism

a. That Dubois was too "piecemeal," must be true; but is not von Bonin perhaps too "wholesale"?

While we have no device for measuring, for instance, the intelligences of gorillas and lions (they are approximately equal in body size), I, for one, am reluctant to believe that the larger size of gorilla brain means nothing at all in the matter of relative intelligence. One does not have to accept the Brummelkamp scale of $a \log \sqrt{2}$ before being aware that, on a field such as those of our FIGURES 15, 16, 18, 20, animals of comparable body size do seem to follow some rational scheme of brain size. Thus, edentates are lowly as compared with carnivores; so are marsupials; Primates are very high; Reptilia and Amphibia are exceedingly low.

If we are content to draw an axis of slope .66 through the entire mammalian constellation, we cannot avoid wondering about a certain parity of cephalization coefficient among all forms, at a given distance above it or at one below it. That would throw together some very small and lowly animals with some very large and specialized ones. This, of course, would not vitiate von Bonin's system; but it certainly would give the whole problem of relative brain weights a different orientation. What is this orientation?

b. A second deterring thought comes from the first. Very shortly, we shall offer a system of curved lines that pass through the mammalian constellation, but which, in the greater part of the constellation, will be very gradual. Now, if this possibility be granted, pending its demonstration, then we may say that von Bonin's test for rectilinearity gave a spurious result. That test simply reported that the *chances favored* a straight-line axis over a curved one; but it did not eliminate—and von Bonin does not claim it did—the lesser chance. In the present instance, we shall soon attempt to show that the "lesser chance" obtains.

c. Von Bonin, in practice, disregards the potential testimony of each taxonomic subdivision in the constellation. I have termed this a "wholesale" method of solution. FIGURE 21, which reproduces his tables and agrees, therefore, with his own illustration (*ibid.*) is composed of the following entries: 40 primate species (23 genera); 9 prosimian species (5 genera); 3 insectivoran genera-species; 4 chiropteran species (3 genera); 18 carnivore species (12 genera); 17 rodent species (15 genera); 12 ungulate species (10 genera); 8 cetacean individuals (7 species in 6 genera); 4 edentate species-genera; 4 marsupial species (3 genera).

This is certainly no balanced ration. If the mammalian constellation actually contains trends such as that proposed by Brummelkamp, or that to be developed shortly, this representation would conceal it.

d. Moreover, in the figure by which von Bonin illustrates the mammals, he omits the line that should graph his formula. Therefore, in FIGURE 21, I have added it to the plot. Obviously, it does not fit the data in the lower-left end of the constellation. Had the data been such as to secure equitable representation to all mammalian orders, this would have been even more noticeable. The only way that it could be achieved would be by weighting the data. This von Bonin did not do.

What I consider to be the shortcomings of von Bonin's solution, and those of the solution developed by the Dubois school, will be understood better if we now turn to an alternative—and this the more, because first, it developed out of a growing dissatisfaction with the Dubois view. Then, and only after it had been formulated out of all the raw data I could find in the literature, von Bonin's study came to hand. That study challenged to a careful review.

We may now turn to an alternative hypothesis. From its standpoint, we shall also try to reinterpret some of the phenomena indicated by Dubois and his followers; after that, we shall reconsider the data of von Bonin.

C. THE EXPONENT OF CEPHALIZATION

1. The Exponent as a Second-Degree Parabola

Dubois operated by pairing genera or species of closely related animals of unequal body size, but assumedly about equally intelligent. Then, by way of algebra, he did the equivalent of joining their logarithmic dead centers (on a log-log grid, their points $P{:}X, Y$) by straight lines, and measured the slope. Then, believing that these slopes were sufficiently close to warrant it, he averaged them all and obtained approximately $r = .56$.

Von Bonin plotted a large number of points representing (unevenly, as already shown) a comprehensive miscellany of all extant mammals, tested the entire constellation for a rectilinear axis, found the chances favored rectilinearity, and so calculated a single slope for the single mass.

The method in the present study, developed before von Bonin's paper was encountered, proves to lie between that of Dubois and that of von Bonin.

If we plot on a log-log grid an order, a superfamily, or a family (much as Brummelkamp did, but omitting his $a \log \sqrt{2}$ scale), we have a simple scatter-field with some interesting properties. See FIGURES 13, 14, but more especially FIGURES 16–19.

a. Repeatedly, the larger members of a phylum—bears, tigers, lions, elk, etc.—will fall *below* a slope of .56, if a line with that slope be first passed through the smaller members of the same genus or family.

b. It is possible to trace an axis through each of these constellations abstracted from the mammalian whole, and the axis is manifestly curved and concave downward. At the lower-left end of each constellation, the slope is very steep. Hence, Brummelkamp found occasion to mount his scale for the cephalization coefficient. He had assumed slopes of .56 over most of his fields, so that the lower-left end had to be accounted for by way of saltatory increases in the coefficient. However, he never tried to explain the reverse phenomenon at the upper-right end: the falling-off in cephalization level there, once parallels of .56 have been superimposed upon the field. On the other hand, there is no way of explaining any curvature whatever, once von Bonin's straight line be granted.

c. If the data now be reassembled, as in FIGURE 20, we seem to find a *sheaf* of curved lines, all concave downward, and the steeper the elevation of the line, the more sharply curved it is. (See also FIGURE 22.) Immediately, we realize that no scheme of .56 slopes could be justified in the primate portion of the total constellation.

Thereby, a family of parabolas $Y = A + bX - cX^2$ suggests itself, in which the relations between b and c determine the slopes of each and all. The $- cX^2$ becomes a correction-term to the straight line $Y = A + bX$ (whether of the Dubois or of the von Bonin system) to take care of the downward concavity: the defection of the larger animals at the upper-right, and the steep ascent among the smaller animals at the lower-left.

2. Other Forms Tested

Further considerations, I think, will strengthen the choice of the parabola. Meanwhile, it is well to note briefly that other types of curve have been tested, but found less satisfactory:

$$y = ax^b, \qquad y = ax^b + c, \qquad x = a\epsilon^{by} \qquad \text{or}$$

$$y = \frac{\log x - \log a}{.4343b}, \qquad \text{and} \qquad y = a + bx + c \log x.$$

(In all these cases, y and x are general terms for the formula types. Naturally, we should substitute Y and X). While this far from exhausts the possibilities, it does narrow the choice.

We turn now to descriptive analyses of the mean trends or axes in the primates, the carnivores, and the artiodactyls.

3. The Primates

a. It is not unreasonable to suppose that man has risen from some ancient catarrhine monkey form, although discussion of the point does not belong here. In qualitative comparative anatomy, the catarrhine monkeys, especially the *Rhesus,* are stock material for showing evidence in the matter. The *Rhesus* is considered by some to be a rather generalized extant form, and therefore furnishes a convenient point of departure. In quantitative comparative anatomy, however, as has been stated already, an appeal from a *Rhesus* to *Homo* is much less safe. For it has not yet been shown that *Rhesus*—specifically, in the brain/body weight relationship—has stood still from the Tertiary day when the *Homo* line began to draw away from some common catarrhine field. The cercopitheques—at least, their less evolved, more generalized forms—quite reasonably may lie closer to the common ancestor than does *Homo;* nevertheless, proximity is not identity. More specifically, we do not know that, when man's true ancestor was the size of a *Rhesus* macaque, his brain was the size of a *Rhesus'* brain.

But since we are making a study in quantitative comparative anatomy (quite confessedly, in the hope that it may furnish some groundwork for later, truly phylogenetic studies) we shall find it convenient to appeal to the catarrhine monkeys. Now, they vary widely in brain and in body size. But we need some dead center. After weighing the factors, I have chosen the mean brain and mean body weight of my cercopithecid data, but omitting the Cynocephali because of their obviously high specialization. The choice, therefore, is subjective, and future events must be its judges. Hereinafter, "Cercopithecidae" shall be the (unfortunate) term used to mean these monkeys, with the Cynocephali omitted and treated separately.

By extension and speaking the same way, the primates are descended from insectivores. We have no comprehensive data on these, but Crile and Quiring give the means of 68 shrews, which are very small animals.

There are a few other scattered data of insectivores; but in a log-log plot they would not fall far away from the shrews. In the present experiment, let the shrews suffice.

The point for man is from the pooled adults (sexes combined) of the data of Crile and Quiring. Their list includes individuals of various "races."

The three points—*Homo*, Cercopithecidae, *Blarina*—are joined by a curve, concave downward, expressible as a parabola having the formula

$$Y = -2.2417 + 1.549X - .0899X^2$$

or

$$y = .005732x^{1.549-.0899\log x}.$$

While any three points can be connected by a parabola, it is immediately striking that the marmosets, the Cebidae, and the baboons three discrete points—range themselves very close to the curve. See FIGURE 15 and TABLE 19.

The straight line $Y = A + bX$ is but the central case of

$$Y = A + bX \pm cX^2;$$

for there, $c = 0$. The antilogarithmic equivalent of $Y = A + bX$ does not have to be written $y = ax^b$; it may also be written $y = \text{antilog}_{10} (A + bX)$, or $\varepsilon^{2.303\,(A+bX)}$. Similarly, and for convenience, let us write $y = \text{antilog}_{10} (A + bX - cX^2)$, or $\varepsilon^{2.303\,(A+bX-cX^2)}$, and call

$$A + bX - cX^2$$

the exponent of cephalization.

b. As striking a feature as any in the primate line is the spacings between the several stages of animal types. They are listed in TABLE 20. The ratios between man and baboon and between man and Cercopithecidae are the *lowest* in the list: *i.e., the greatest proportionate rises of log brain to log body weight occur anywhere but between man and the forms next below him.* (Incidentally, these ratios correspond to the formula

$$\frac{\log E - \log e}{\log P - \log p} = r.$$

In the case of baboons/Cercopithecidae, one might have presupposed "equal cephalization" and hence have expected $r = .56$, provided the Dubois scheme be correct.) This progressive loss of slope is a crude indication, if such be needed, that the several morphological levels are joined by a curve concave downward, whatever be the actual type of formula that fits it best.

At least one thing is certain: there is nothing "aberrant" or "exceptional" about man's cephalization, unless it be the fact that he occupies one extreme of the mammalian front. By such definition, the extreme would always equate with aberrant, no matter what the animal might be.

c. Granting the *Homo* line of mean tendency, how broad a band on both sides of that line would be tolerable for the variational proportions of man and of his sub-human lineal ancestors?

In FIGURES 15 and 20 is an enclosure or a line indicating a tolerable range in the brain-to-body logarithmic ratio for *Pithecanthropus erectus.* (Brain weight has had to be estimated from cranial capacity. For a discussion, see Martin (1928), II: 743f. There, these figures occur for modern man:

	Brain weight ratio of gm/cc	Cranial capacity
Welcker 1886	.91 at	1200–1300 cc
	.95 at	1600–1700 cc
Bolk	.737–.94 at	aet. 30 years
Manouvrier	.87	general average

Experiment with figures in the literature has led me to adopt .876 as a workable figure).

Some data on Palaeanthropoi are assembled in TABLE 18. Unless otherwise indicated, the brain weight estimates are my own. The cranial capacities are taken from Hrdlicka (1930), except for Weinert's, which is from his *Ursprung der Menschheit.*

The reader may shift about these "brain weights" on the charts *ad lib.*, to try them with different putative body weights. Now, if increase of brain weight demands a certain increase of body weight and increase of brain complexity demands a certain increase of brain weight (This seems to be a cardinal implication of our chart, so that a creature of gibbon size, yet with the brain complexity of a man, seems ruled out as a normal thing, despite the occasional occurrence of Tom Thumbs), then *Pithecanthropus erectus* cannot be ancestral to extant man. His body is too large for his brain, just as, to a more exaggerated degree, that of an ape is too large for his brain to represent or reflect the subhuman proportions of any ancestor of man. In terms of the graph, it seems too much to demand that the *Homo* line pass first through *Pithecanthropus*, then suddenly take a geniculate turn vertically upward. As a matter of speculative theory, when a body develops ontogenetically, it budgets a certain proportion of its total growth-energy toward developing the size and complexity of its central system of control. The present study supports the notion that the budgetary balance between the total growth-energy of the soma and that portion appropriated to brain is too fundamental in the biological economy of the organism to allow the total body to remain phyletically stationary in size, while the brain growth budget is revised drastically upward. Rather, the alteration of the brain-to-body ratio is conceived as being impossible without concomitant alteration of absolute size in both body and brain. This is the obverse and reverse of a common biological fundamental. When man's direct ancestor had a brain the size of that of *Pithecanthropus*, his body was smaller: according to the *Homo* parabola, about 40,000 gm. But what the *complexity* of that brain would have been, as compared with that of *Pithecanthropus*, there is, of course, no telling.*

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* See "Addendum" at end of Section IV.

4. The Carnivores

We assume:

(a) The carnivores are derived from small insectivores.

(b) Among progressive stocks, the smaller (carnivore) is more likely to be the conservative member of his group: *e.g.*, of the Felidae, with their great body range, the smaller cats will be nearer the ancestral proportions than the larger ones. Likewise, among the Procyonidae, Canidae, Ursidae, the first will be most nearly of ancestral proportions. These assumptions may be false, or only inaccurate; nevertheless, the experiment is worth trying.

From Crile and Quiring's adult racoons, weasels, and the same shrews as before, we obtain the parabola:

$$Y = -1.9227 + 1.283X - .0844X^2.$$

See FIGURE 17. The points in the figure are the data of TABLE 15, their numbers being those of the entries in that table. None of the specimens beyond 15 (*Procyon lotor*), to say nothing of most of those below it, have had anything to do with formulating the line. Yet I do not believe one could ask for a better fit.

5. The Artiodactyls

FIGURE 18 shows them running approximately the same course as the Carnivora, suggesting that the modern survivors of these two orders (both of which have creodont ancestry) have been running neck-to-neck in an evolutionary race: predator and prey, balanced thus far, so that the former has not exterminated the latter. However, the Tragulina are placed a little too far to the right, just as the lemurs are, to fit a parabola of mean tendency. The gap between the shrews and the smallest antelopes is too great for a primary case in demonstration. Now, however, with the Carnivora so amenable, an essay on the artiodactyls is fairly safe. The Antelopinae are represented by a great body range. So, taking the shrews, *Cephalophus*, and the three genera 8, 9, 12 (TABLE 13), which are clustered, we obtain:

$$Y = -1.9284 + 1.289X - .0838X^2$$

and the curve is in FIGURE 19. From TABLE 13, the other points are added as checks. The line is practically identical with the carnivore.

6. A Criticism of the Curvilinear Cephalization Exponent Based upon the *Homo* Line

Consider FIGURES 15, 17, 19, 20.

a. It is as important to understand what the *Homo* parabola is not, as to understand what it is.

It does not represent an *average* trend among primates, but rather some kind of higher extreme; a line by which man can be reached. Had we used Hrdlicka's (1925) orangs, instead of Crile and Quiring's humans, we would have had, out of otherwise the same data:

$$Y = -2.6925 + 2.0518X - .2007X^2.$$

(The orang values of $x = 54507$, $y = 335.7$ were obtained from the unweighted average between means for 8 male and 12 female adults.) On the other hand, the lemurs occupy, far down the scale, a position relative to the *Homo* parabola analogous to that held by the orangs, far up on the scale, relative to the same *Homo* parabola; but we would not be justified in trying to pass a lemur parabola through the Hapalidae, as we have done with the orang and *Homo* lines.*

The scatter-field of adult Cercopithecidae in FIGURE 15 shows what tremendous latitude in brain/body weight ratios exists in the primate constellation; or, what a wide range in the constants of b and c should exist among primates. This is a problem in variance. When coupled with analogous data in other orders, it carries this study into more advanced levels which cannot now be explored. But let us state carefully that, in spite of all the parabolic treatment in this study, we must *not* imagine the differential evolution within the primate stock as following a set of discrete parabolas, so as to make man ascend strictly by way of one trajectory while the orang has followed another close by. We cannot be such purists as to imagine that to be the case. Rather, what we are attempting to develop is the picture of a *band* in the primate portion of a total mammalian constellation, having parabolic curvature, and a breadth as yet undetermined at any point along its course. That band might be visualized as the limiting outline of a whole sheaf or spray of parabolas having various inclinations and curvatures. But even that would be a fictive device for trying to grasp the biological entity behind it. That entity is one of range in variation of body-to-brain weight throughout the entire period when primate genera and species are gradually evolving and differentiating. The mechanism is, of course, that of unceasing matings and breedings of countless individuals. The proportions peculiar to man or peculiar to orang, etc., finally emerge, but even they have a range tolerance in the matter of brain and body weight. The *Homo* line is an *axis of mean trend for attaining man from out of the insectivores.* The axis is a line on which, *for purposes of calculation,* we may consider all entry points to have been clustered. It is an *"as if"* line. At any level within the primate band which is below both the definitive human and the ape and, therefore, by right of title common to both, if we had the requisite data on their ancestors, those ancestors probably would be all mixed together, and identifiable at some differentiating epoch only by the qualitative taxonomic methods of the paleontologist. Quite conceivably, however, if we did have all these ancestral entries, when we stand at the spot where the population is about to differentiate the humanoid and the anthropoid, those destined to be progenitors of man might tend to be more frequent on the upper side of the primate band, while those destined to produce apes might trend towards concentration on the lower side. Whether this speculation be justifiable, probably must remain unresolved for a long time.

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* FIGURE 15 amply demonstrates why it was but an accident that Dubois obtained a slope of .56 in his Primates, when he paired the orang and the gibbon.

b. Necessarily, in the carnivores and artiodactyls, we should have to explain the positions of such forms as Tragulina and Mustelidae in the same way that we have handled the Lemuroidea, the Anthropoidea, and the Cercopithecidae. The Cercopithecidae, Mustelidae, and even the Lemuroidea have their own local axes lying athwart the parabola of the cephalization exponent. They recall Lapicque's dogs and his ontogenetic exponent in its position relative to the phylogenetic slope of .56.

7. A Line of Mean Tendency in Modern Mammals

None of the other orders, not even the rodents, which are well represented in point of genera, but which present certain peculiar difficulties, yields as ready returns as the three foregoing orders. Yet parabolas can be fitted to them that are consistent with those three. Later on, we shall do this (TABLE 26), but such testimony cannot be used to establish the case of the parabola.

On the other hand, the entire mammalian constellation does lend itself to calculating the mean trend of *extant* mammals. The method here followed has attempted to weight the various genera equally. After a formula has been calculated from my own collection of data from the literature, the experiment has been repeated on von Bonin's collection.

Consult now TABLES 24 and 25.

The theory underlying the method is simply this. Each animal kind is considered as representing a situation. Thus, no matter what its success or failure in breeding large numbers, or even in differentiating species out of a genus (surely the brain-body relationship could not differ palpably among species of one genus), the brain/body weight relationship is a biological reality. Now, Dubois and his followers used mostly the genus as a unit of comparison. It should be safe to make all entries in terms of genera. Nevertheless, we really should have the same number of genera in each order, if it is orders that we wish to formulate. So I have applied this formula:

1. Take the *mean* of a *genus* as the unit of entry.

2. Count the number of genera in each order. Let the number for the most numerously represented order be standard.

3. Divide this number by the number of genera in each of the orders, to obtain a multiplier or operator: *i.e.*, let C be the greatest number of genera in the best-represented order, and N be the number of genera in any one of the others. Then,

$$\frac{C}{N} = W,$$

and W is the operator by which to weight each Y and X in the order. Now, a genus occurs in a certain spot on the graph. The orders are more densely represented in one part of the field than in another. We wish an even distribution. The range of X is therefore divided, at intervals of .5, into 11 classes, and all the genera within each area so defined, no matter what their orders, are grouped for an average. For instance:

GROUP 3

Genus No.	W	WX	WY
12	1.304	3.020	1.180
13	1.304	3.060	1.100
23	1.304	3.240	1.270
40	1.304	2.870	.924
74	1.	2.484	.774
75	1.	2.201	.613
90	1.	2.301	.201
96	1.	2.033	.452
N = 8	Σ = 9.216	Σ = 21.209	Σ = 6.574

$$\frac{\Sigma WX}{\Sigma W} = 2.304 \qquad \frac{\Sigma WY}{\Sigma W} = .714.$$

These two quotients stand for the "dead center" of Group 3. A parabolic formula can then be calculated from the 11 groups.

In making my revised calculation, after reading von Bonin's paper, I added his insectivore genera to mine; also, I excluded *Balaenopterus*, as he had done, but saw no reason for excluding *Homo*. Furthermore, since the species of *Felis* cover so wide a range, and von Bonin lists them as several genera, I grouped them into four body-sizes and let these stand for genera. Von Bonin lists *Asinus asinus* as a genus, while I left it *Equus asinus*. In handling my own data, I could not bring myself to make a separate order of the Prosimiidae; although, in calculating von Bonin's collection, I left them separate to conform with von Bonin. My own collection contains at least 116 units (tantamount to genera), namely:

23 Primates, 23 Carnivora, 22 Ungulata, 30 Rodentia, 3 Pinnipedia, 2 Cetacea, 4 Edentata, 4 Chiroptera, 5 Insectivora.

Then $C = 30$, and each of these numbers equals N, whence in each we obtain $\frac{C}{N} = W$. At last, the formula is:

$$r = -1.808 + 1.154X - .0543X^2.$$

See FIGURE 20. It seems a very fair fit.

Repeating on the 82 units or genera of von Bonin's list less the giant Cetacea and less the 3 marsupials, which are not Eutheria, we obtain, from 79 units or genera:

$$Y = -1.4045 + .8724X - .01363X^2.$$

See FIGURE 21.

The data of von Bonin give a flatter parabola, but the first passes closer to the Balaenoptera, which were included in the calculation. The first also converges better with the ordinal lines at the lower-left end.*

We have observed previously that statistical tests for the rectilinearity or curvilinearity of a constellation (such as the mammalian of FIGURE 20 or of FIGURE 21) simply measure a *probability* of the condition being the one or the other. These tests do not *eliminate* the alternative possibility. But before we can penetrate further into the problems actually confronting us, we are in duty bound to test our own mammalian constellation by the conventional methods.

In this matter, we shall have to give to the genera of each order their weightings as per TABLE 24, then calculate the correlation coefficient r and the correlation ratio η and use one of Blakeman's tests for a significant difference. We obtain:

$$Y = +.966 \qquad \eta = .969.$$

Applying now the formula,

$$\frac{d}{\sigma} = \frac{\eta^2 - r^2}{2\sqrt{\frac{(\eta^2 - r^2)[(1 - \eta^2)^2 - (1 - r^2)^2 + 1]}{N}}},$$

---

* In FIGURES 20 and 21, there appears to be too heavy a field below the curves. But marsupials and extinct mammals have been entered in the field without being included in the formulation. A further distortion, not measurable to the eye, comes, of course, from the use of the frequencies W of TABLE 24.

we obtain .624, which is not a significant figure. Therefore, if all there be behind the constellation is only a statistical correlation, von Bonin is right: the axis is probably rectilinear.

But since we have approached the analysis by way of orders or stocks, where any line that passes through their samples is manifestly curvilinear, the question is legitimate: Cannot their aggregate permit a *deceptively* straight line to be drawn through the whole?

My own belief is that the rectilinear axis is a deception. Let us recall some descriptive remarks from the discussion of "pseudo-phylogeny" (Section III, Subsection 2, Preliminary a) and picture in somewhat better detail the upsurging of the true "phylogenetic" lines through the pile of transparent sheets representing the past epochs with their now-fossilized forms. In this connection, it is rewarding to consult FIGURE 13, the ungulate scheme reproduced from Brummelkamp, and note the positions of the small, white circles that are entries of extinct forms; also, anticipatorily, FIGURE 22, where *Diplobune* and *Anoplotherium* are again entered. In the scheme we are now imagining, these extinct forms (and countless others analogous to them) would not occur on these surfaces actually before us, but would be buried somewhere in the depths of our pile. Using the artiodactyls as an example, the indication is that, if we had all the curves on all the sheets of our pile, they would generate a curved *surface*, standing on edge, so to speak, and cutting upward through the pile of sheets: a surface located in the third, or z-, dimension. Moreover, the now-extinct forms seem to describe curves in which the brain weight is less, relative to body weight, than it is in extant forms. In other words, as we come up through our pile, the curves also tend successively to become more elevated with respect to the y-axis. Modern ungulates have a higher brain/body weight ratio than extinct ones.

Now, with this element of behavior in mind, consider the diagram of FIGURE 22 as a whole, and consider it as the top sheet of the pile. Then, in the lower-left region, there still exist mammals of comparatively low cerebral organization, sloths, kangaroos, *et al.*, which are also relatively small in body size. Peering down through the pile, however, we perceive giant sloths, glyptodonts, kangaroos, wombats, and many others, such as *Baluchitherium*, *Uintatherium*, the last of the titanotheres; to say nothing of Irish elk, the Imperial elephant, *Megaladapis*, and *Gigantopithecus*. It is evident, then, that, unless a phylum produces members of ever higher proportion of brain weight, its only representatives that survive eventually are animals of relatively small size; otherwise, the entire phylum becomes extinct. If, then, we had all the lines of all the orders from at least early Tertiary to Recent, they would shape for us a block as though it had been carved. It would be curved in a way hard to describe. It would be standing on end, and leaning at an angle. As we look down upon it, through our pile of transparent sheets, we get the impression of a "cliff" facing down and to the right: a face where Nature has eroded away the surface that would have been formed by the aggregate of the right ends of the lines, in that region, the lower-right, where large body and small brain would occur. For marsupials, edentates, rodents, Chiroptera, Hyracoidea, are represented at long last, on top, only by small forms, while Multituberculata, Tillodontia, Amblypoda, Notoungulata, *et al.* are completely extinct. The most highly cephalized line, that of the Primates, which belongs to that surface of our model that faces *up-and-left,* does not contain, and never has contained, the largest of all mammals in point of total body weight.

Add now the complication that each of the lines, and the surfaces which we are imagining that they generate by their close contiguity, is but an axis of means. To each side of each line should lie an accompanying province for everything that deviates from the mean.

In short, had we carved a block of wood to represent the history of cephalization in mammals, its scheme of construction might be made up completely of a system of curvatures; then, as we whittled or sheared off a large chip representing what the extinct lines would have become had they been allowed to continue, we might well have ended up with a certain surface on our top sheet, the shape of which would permit us to calculate a certain long axis for it. This straight-line axis then should be, I think, the regression-line calculated by von Bonin.

Meanwhile, by confining ourselves to the much-trimmed plant that still survives, we can obtain, I think, some idea of the range in log brain weight that exists today with respect to the range in log body weight. Using as arrays of Y the eleven groups we have formed by dividing the scale of X at intervals of .5, we can obtain a σ for the mean of each array (M_Y). The regression of σ_Y on X is:

$\sigma_Y = .2072 + .01756X$ (unweighted by the operators W);

or $\sigma_Y = .2547 + .00539X$ (weighted as in $\Sigma f \cdot \sigma_Y = \Sigma f \cdot a + \Sigma fX \cdot b$, where $f = W$ properly applied to each genus.)

Thus, the standard deviation increases practically not at all as X increases. If, then, σ_Y of each array be divided by the M_Y for that array, the quotient CV_Y follows a very regular negative parabola:

$$CV_Y = 1.699 - 1.3135M_Y + .2545M^2_Y,$$

so that the range of variation in Y narrows rapidly with increase of Y and X in the extant mammalian constellation. (At $M_X = 2.304$ and $M_Y = .714$, $CV_Y = .374$; at $M_X = 6.23$ and $M_Y = 3.2035$, $CV_Y = .0903$.) This is not unexpected. For, as FIGURE 20 shows, with rise in X fewer and fewer orders participate: as we have just been saying, they never produced giant representatives, or else their giant members have become extinct. Nature has not been indefinitely patient with big bodies plus small brains; nor, for that matter, has she ever produced superlative brains in superlative body sizes. Neither has she produced superlative brains in tiny bodies.

D. A STATISTICAL ANATOMY OF THE MAMMALIAN CLASS, ASSUMING THE VALIDITY OF THE EXPONENT OF CEPHALIZATION

INTRODUCTION

1. The adoption of $Y = A + bX \pm cX^2$ as the type-formula for representing the relationship between brain and body weight is, then, frankly empirical only. Whether it can be rationalized theoretically, I do not know. At least, as will develop soon, it yields certain further results that are consistent. This much, I think, is already reasonably secure: the axis of mean tendency in order or class is a curve, concave downward, and therefore changing slope at every point.

From now on, we shall behave *as if* the second-degree parabolic formula were the most acceptable type and explore the consequences.

2. The formula $Y = A + bX - cX^2$ is analogous to that of a shell trajectory, which is often written $T = s_0 + v_0t - \frac{1}{2}t^2$, where T is the trajectory, s_0 is the initial distance or position, v_0 the muzzle velocity, t the time, and g the gravitational force. But in the exponent of cephalization, discrete factors cannot be so isolated and labeled. On the other hand, if the Mammalia originated from reptiles, their parabolic exponents, which (in FIGURES 20, 22) spray outward and upward and to the right, presumably must have had an "initial distance." Later on, we shall try to render this particular a little more precise. For the present, we shall study the relations between the terms containing X.

The correction term cX^2 progressively subtracts from what otherwise would be a rectilinear slope. Hence, *whatever be its biological antecedents, if it has any,* it is the analogue of $\frac{1}{2}gt^2$, and $c \equiv \frac{1}{2}g$, or $2c \equiv g$.

The velocity of the exponent of cephalization is, of course, given by:

$$\frac{dY}{dX} = b - 2cX.$$

The value will be greatest for the smallest of the mammals. In fact, as we shall see later, the closer we come to a reptilian level in the general region of which the mammals presumably departed, the greater is this velocity.

The velocity, at any given value of X, is highest in the primate parabola. It departs farthest from the mean of mammals on the plus-side. This adumbrates that aspect of the problem, again, which deals with the variance, but we shall postpone that aspect. For the present, an indication of the comparative velocities of the various parabolas can be had by finding the point at which the rate of increase in log brain weight has fallen to equality with that in log body weight; that is, where the slope of the parabola = 1, or forms an angle of 45° with the abscissa. Let us call that the point of *isauxon*. Then, when $b - 2cX = 1$, X equals:

in the *Homo* line,	3.05
in the carnivore line,	1.63
in the antelope line,	1.72
in the mean mammalian line,	1.42.

The primate isauxon point occurs, then, comparatively late, somewhere between the hapalid mean ($X = 2.44$) and the cercopithecid mean ($X = 3.30$). The shrews occur at $X = 1.2396$, before these isauxon points, and therefore presumably in a region where, when the early primitive mammals existed, the log brain weight was still increasing faster than log body weight. The deceleration $-2cX^2$ had not yet brought the velocity down to 1. This comments on the original and elementary phenomenon that was partly responsible for the investigations of Manouvrier, Snell, Dubois, and the others of their day: the brain weight/body weight ratio of some Insectivora is greater even than that of man.* But the present explanation obviously differs from the solution of Dubois. And the mammalian scheme, a falling-off in the ratio as animal bodies increase in absolute size, will later on be found to contrast with the reptilian scheme.

At the same time, FIGURE 20 demonstrates that the most highly evolved of the mammals tend to occur even more to the right and higher up. *Cerebral organization, thereby, seems to demand an absolute increase in body size to support it.* Yet this increasing cerebral complexity goes with a falling ratio of log brain weight to log body weight, so that even giant man rises no higher in brain weight per body weight than his putative insectivore ancestor.

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* More precisely and graphically, if a slope of 45° be passed through the Hapalidae, even the primate slope loses height rapidly enough to place man below that line. In marmosets, the ratio of brain weight/body weight is .039; in man, it is .021.

This is but a statistical comment to some very profound and obscure neurological processes among the mammals.

Almost as striking is the further fact that the body-size range of 1000–10000 gm. includes the bulk of extant mammalian types and an extremely wide range of cephalization. It appears as a sort of focus. Beyond it, to the right, is a region once held by mammals now extinct, and above that region one which has been "settled" in latter ages by the more specialized, large-bodied, extant forms. In this region, the large artiodactyls and carnivores now appear as close to the bottom of cephalization for mammals of that magnitude, because the archaic giants are extinct. This partial erasure of the mammals on FIGURE 20 is but a reflection of the psychic-armament race which the class has been conducting intramurally.

E. THE REPTILIAN SUBSTRATUM

1. A Reptilian Cephalization Exponent

FIGURE 20 suggests that, with fuller data, we might reasonably expect other ordinal parabolas after the fashion of those just presented. A little later, we shall attempt what is frankly an approximative reconstruction of several. Before that, it is desirable to relate such parabolas as we already have to a possible reptilian line.

For this experiment, we have the data which Dubois and others used in obtaining the phylogenetic exponent and the cephalization coefficients of reptiles (and of amphibians). (See TABLES 21, 22.) These are extant reptiles, just as the mammals we are using are extant.

It will be noticed (FIGURE 20) that, in their brain/body weight proportions, the smaller reptiles are identical with Amphibia. In spite of the higher morphology of the reptile, the size of its brain is not sufficiently heavier than that of an amphibian of equal body size to register a significant difference on the graph.*

It will be noticed, further, from TABLE 21 and FIGURE 20, that the reptiles localize rather definitely by their classes, so that, even if we were to follow Dubois' system, the mean cephalization coefficients would tend to separate them as Crocodilia, Lacertilia, Chelonia, Ophidia, in that order. None the less, the range of the individuals within the one order Crocodilia is relatively large.†

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* Brummelkamp gathered his Amphibia (they are all Anura) into three groups, according to mean values of k: .01799, .01317, .009391. (These give logarithms which, when divided by log $\sqrt{2}$, yield $\alpha = -13.46, -12.5, -11.6$; which, to be sure, differ by approximately 1 whole unit.) The reptilian mean values of k range, as TABLE 21 shows, between .0222 and .00927.

† In terms of k, it is 1.659; or, on Brummelkamp's scale, in terms of log k it is .2198—*i.e.*, 1.460 log $\sqrt{2}$; *i.e.*, a is nearly 1½. This is more than 1 and less than 2 units of a. I do not know how Brummelkamp would explain such a high range of saltation.

We compute a parabola from extant reptiles, for comparison with the mean parabola of extant mammals. We obtain, from all the data of TABLE 21,

$$Y = -1.7095 + .3679X + .03613X^2.$$

This is concave *upward:* the log brain weight *accelerates* as body size increases.

Under the Dubois system, this same phenomenon would have to be interpreted as a rise in cephalization coefficient, so that the Crocodilia would stand highest and Ophidia lowest. (Note, however, that the data do not include large Chelonia or Ophidia, such as the great sea tortoises, pythons, etc.)

For further comment on the positive curvature to the reptilian parabola, see Section III, F 2 a, Addendum.

2. Intersection of Mammalian and Reptilian Exponents

FIGURES 20, 24, *et al.*, demonstrate the fact that the mammalian parabolas intersect the reptilian in a region of very tiny reptiles.*

The lower intersection of the two equations:

$$Y = -1.7095 + .3679X + .03613X^2$$
$$Y = -1.8080 + 1.1540X - .0543X^2$$

is $Y = -1.6624$, $X = .1267$. Allowing sufficient latitude to make this point the indication of some limited region, we may still conclude that the mammals must have diverged from some tiny-bodied reptilian stock. The origin of the impulse to devote a larger percentage of growth-energy to brain development must, therefore, have been possible only in bodies of small size. That plasticity is not to be looked for after reptilian bodies have increased beyond some rather modest point. But just where that point was, cannot be said.

Pending, then, any modifying testimony from fossil forms, the data of extant mammals and reptiles indicate that:

Relative brain weight *increases* in reptiles as body size increases;

The animals that eventuated in mammals were small creatures that initiated a markedly accelerated growth in weight of certain parts of the brain;

The acceleration was related to increase of body weight in such a way that increased complexity, particularly of certain parts practically absent in the reptiles, thereby became possible; or, stated conversely, without increase of body size, there could have been no increase of complexity such as has taken place;

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* Indeed, it is possible that, had we the requisite data from fossil forms, including the theromorphs, the divergence of the mammals from the reptiles by way of a sprouting neocortex would give the mammalian curve an S-shape with a very short lower limb. The parabolas we are tracing would then be merely the very long upper limbs from an equation higher than the second degree. This, of course, would not vitiate the present development; it would but correct and amplify it.

The rise in log brain weight with respect to log body weight was most rapid when and where the mammalian stock was early, small, and primitive;

Yet the increase in mammalian brain weight has been moderated by a steady subtraction from the logarithm of brain weight expressible as $-cX^2$, where $X =$ log body weight.

When compared with the reptilian behavior, the mammals have taken a peculiar shortcut to large size of brain, which, because it concentrates on certain areas very much restricted in the reptiles, has passed from the quantitative to the qualitative.

There will be a little more to say about this later on. At the moment, this mammalian preeminence and the shape of the curves by which it is traced raise a new and interesting problem. Rather, they place an old problem in a new light:

3. Weights of Mammalian Brain Stems and Weights of Reptilian Brains

If, for want of something better, we roughly term the mammalian brain "neëncephalic" and the reptilian (and amphibian) "archencephalic" we might ask whether, if it were possible to isolate the "archencephalic," portions of the mammalian brain, they would prove to have also participated in the mammalian upsurge, or whether they have rather tended to preserve an archaic weight relationship to the body as a whole.

The question, of course, cannot be answered at all accurately. Nevertheless, the following experiment is suggestive.

Data exist on the weights of mammalian brain portions as divided by the knife. While the comparison obviously is not more than partially correct, we may consider the "brain stem" of some mammals, beside what the total weight of brain would be in a reptile of equivalent body weight, the reptilian brain weight being computed from the parabolic formula just obtained.

a. Starting with man, we have data from Marshall (1892) who constructed from Boyd's tables (in pounds and ounces) the mean body weights and mean weights of total encephalon, cerebrum, cerebellum, and pons-plus-medulla. (See TABLE 23, which abstracts from Marshall.) Boyd's people were clearly undersized of body, so that our computed ratios in column VI presumably are a little high. Anthony (1928) states the ratio to be 2 per cent. We shall use the operator .0206, the average of mean male and mean female of TABLE 23.

Applying it to the mean brain weight of Crile and Quiring's humans —1320.15 gm—we obtain 27.22 gm for pons-plus-medulla.

Anthony (1928, p. 92) reproduces Manouvrier's calculations from Broca's Parisians:

Stature	154 ♂♂	44 ♀♀
	1680 mm.	1583 mm.
Weight of encephalon	*1361.5 gm.	1201.3 gm.
Weight of hemispheres	1191.0	1045.44
Weight of cerebellum	145.2	131.7
Weight of pons	19.51	17.8
Weight of medulla	6.805	6.36

* There is a small mistake somewhere. The parts add up to 1362.5.

The calculated quantity, 27.22, agrees well with the measurements in this table (pons-plus-medulla).

From this table, the ratios of medulla weight to total brain weight are: males, .00500; females, .00529.

Body weights are not given in these data. But now we can appeal to Crile and Quiring's data, thus:

	♂	♀
Brain weight	1350 gm.	1214
Body weight	65544 gm.	49755 gm.
Calc. medulla weight:		
.00500 x 1350	6.75 gm.	
.00529 x 1214		6.425 gm.

These medulla weights agree well with Manouvrier's figures.

b. We add the domestic cat. The data are abstracted from Latimer (1938):

	52 ♂♂	52 ♀♀
Brain weight	27.56 gm.	26.54 gm.
Medulla plus pons	1.86 gm.	1.79 gm.
Brain/body weight	.01031	.01126

c. Finally, we bring in the albino rat, from Donaldson's (1924) Tables 140 and 144:

Brain weight at 150 days:	1.933	gm.
Body weight when brain weight = 1.933:	259.1	gm.
Brain "stem" weight (encephalon minus cerebrum and cerebellum):	.373	gm.

Let the weights of these portions of mammalian brain be compared with the calculated total brain weights of theoretical reptiles of equivalent size:

	Body weight gm.	Log body weight	Part of brain: gm.	Log of brain part	Reptile	
					Brain weight gm.	Log brain weight
Homo	62080	4.79295	27.22[1]	1.4349		
			6.75[2]	.8293	7.65	.8835
Cat ♂	2668	3.4262	1.86[1]	.2695	.99−	−.0255
Rat	259.1	2.4433	.373[3]	−.428	.254	−.5949

1. Pons-plus-medulla.
2. Medulla alone.
3. Encephalon minus cerebrum and cerebellum.

It is strikingly clear, after due allowance is made for the mammalian pons—which in man is particularly heavy, for certain known reasons—and also for the fact that we are comparing at times only the mammalian medulla with the entire reptilian brain, that the mammalian "archencephalon," if it could be reconstituted, would be of the same *general order of magnitude* as that of a reptile of equivalent size. That the mammalian medulla equates neurologically with the reptilian, is of course an erroneous assumption. But let the figures speak for themselves as far as they can.

One comparison we cannot make, yet it would be more valuable than this arraying of a primate, a carnivore, and a rodent. It would be a comparison of brain stem weights with body weights in several stages within the same order or on the same trajectory; *e.g.*, *Blarina*, Hapalidae, Cebidae, Cercopithecidae, Hominidae. Would a trajectory through these data be concave upward or downward? How would it compare with a reptilian line? If we had such a curve, we could, at all times, measure the vertical difference between the curve for total encephalon and that for brain stem. One need not subscribe to the postulate of "somatencephalon" and "psychencephalon," to consider that the experiment would be suggestive.

4. Discussion and Criticism of the Reptilian and Mammalian Parabolas

Judged on the basis of extant reptiles only, the path of this class curves ever upward, which would mean an accelerated enlargement of brain weight as body size increases. But have we a right to assume by this token that the modern crocodile once had an ancestor of the same brain and body weight proportions as, say, a modern turtle or snake?

FIGURE 20 shows a cluster of amphibians and small reptiles at the lower-left end of the reptilian constellation. The reptiles there are small lizards and snakes. It can hardly be imagined that the trajectory of the crocodilian line did not pass close to this region, but could not that trajectory have been slightly concave downward as readily as concave upward?

The uncertainty about the reptilian parabola actually being concave upward might be illustrated this way. Suppose, among mammals, there survived today only apes, edentates, and insectivores. A curve passing through them would be concave upward, and would be meaningless. When we compute the reptilian parabola on the basis of modern forms, we are dealing with a very fractionated and largely extinct class of vertebrates.

For that matter, this same caution must apply to the average mammalian curve we have computed, although, since the data are so much richer, this curve may carry more value.

In the case of both curves, strictly speaking, they declare simply that, *among surviving forms of the class,* the center of gravity for log brain/log body weight ratio at any given log body size is located at the point $P\ (Y, X)$, and that there is apparently regularity, not whimsy, in the location of these points. The other justification for computing these lines is, that the principles of technique involved would seem to remain valid, even if the raw data were far more complete.

What we need badly, then, is more data, especially reconstructive calculations from paleontology.

Let us repeat once more that, had we more figures for archaic mammals, the modern mammalian constellation would appear as what had been left over from a very extensive erasure of the mammalian block. *Equus* survives, *Eohippus* and *Mesohippus* are extinct. There are two kinds of erasure in the constellation, and their distinctive characters are important in truly evaluating what survives. The ancestor of the titanotheres was transmuted into his descendants, and therefore became extinct only in a transmutational sense. The definitive titanothere became extinct because he ceased to produce progeny. The earliest titanothere ancestor does not appear in FIGURE 18, but in terms of the X, Y axes, quite probably he would be located somewhere to the lower-left, in a portion of the constellation still occupied by extant mammals of entirely other orders. But the titanothere himself would occur in a portion of the field now vacant, as do *Diplobune, Uintatherium, Anoplotherium,* etc. And when the titanothere existed, undoubtedly the portion of the field which once held his ancestors contained forms that were to be the ancestors of certain present-day mammals. That part of the mammalian field or block which today is occupied, say, by elk, grizzlies, whales, apes, and man, was probably still virgin and unoccupied. The axis of the mammalian constellation, therefore, may be imagined as having shifted slowly upward, but maintaining something of a fixed point at the lower-left end.

The situation, *mutatis mutandis*, may have been similar in the reptiles. We are not to infer, from the relatively "brainy" place held today by the Crocodilia, that the extreme dinosaurs would have stood even higher. We cannot tell but that the Crocodilia, exceptionally large as they are among surviving reptiles, owe their present salvation to their (for a reptile) exceptionally large brain system.

Farther along, we shall analyze the ratios between the constants b and c, which determine the elevation and curvature—the velocity—of the various parabolic cephalization exponents. Then, the present-day reptilian situation will add a further and rather striking commentary on this total situation.

So, the fidelity of a reptilian parabola curving positively and mammalian parabolas curving negatively has its pros and cons. But there may be neurological justification for the difference. Actually, we are not comparing neurological comparables, since the mammalian curves are very largely taken up with increases in a portion of brain which in the reptiles does not exist. The reptiles, we might say, the "brain stem" animals. Their increase in brain size, from tiny-bodied forms to giant, is probably necessitated almost exclusively by the much more elemental nervous processes than those having their seat in the association tracts of the mammal. The problem of number of motor and sensory fibers per body size can hardly be discussed here, but Ariens Kappers (1929, p. 198) has said, "Brain weight also depends on the size of body. The influence of body size on the nervous system appears already in the greater number of root fibers of spinal nerves in larger animals compared with smaller ones. So the number of the motor root fibers increases with the transverse diameter of the total musculature, while the number of sensory root fibers increases with the surfaces of the body and (proprioceptive fibers) with the transverse diameter of the musculature." When, therefore, we watch a mammalian parabola rising above the reptilian, and notice the falling-off in the log brain weight which, nevertheless, is taking place, perhaps we should discount further another parabola, buried within this mammalian rise, having a positive curvature similar to the reptilian, which would trace the phyletic growth of that part of the mammalian brain most nearly equivalent to the reptilian.

Accordingly, the foundations of the reptilian formula are very fragmentary, the mammalian only less so. We must make due reservations. Nevertheless, all circumstances considered—especially the principles of method involved—it seems permissible to accept what the formulae say. (For a final comment, see heading F 2 a.)

We return now to the behavior of the b and c constants in the sheaf of mammalian parabolas.

F. THE STATISTICAL ANATOMY OF THE MAMMALIAN CLASS (Continued)

THE CORRELATION OF THE CONSTANTS b AND c

1. The Individual Behavior of the Constants among Several Mammalian Stocks*

On previous occasion, we have drawn the analogy of $2c \equiv g$, $b \equiv \nu_o$, in the missile trajectory, where g is gravity, ν_o is initial or muzzle velocity. But in $Y = A + bX - cX^2$, both b and c have varied per instance. Is the variation regular or random: are b and c correlated or not?

In the case of missile trajectories, the greater the initial velocity (up to an angle of elevation of 45°, or arc tan 1.0000), the greater the horizontal distance covered. The zenith is always half-way over this distance. In the cases of our study, the greater the value of b, the greater, apparently, is that of c, so that the zenith of the highest parabola occurs at the lowest value of X of any parabola.

Before we can be certain of a regular increase (arithmetically) in c as b increases, we must obtain more parabolas. But the less satisfactory condition of the raw data of other orders makes their formulation only a reconstruction. Any conclusions we finally draw must be tempered by this stricture.

We have assumed the right to pass the parabolas of *Homo*, carnivores, and antelope through the field of the insectivores. We have formulated a general mammalian parabola without that assumption, yet it has converged back into the insectivore field. We can hardly be far wrong if we pass other mammalian parabolas through that same region. (To be sure, *below* the insectivore node the parabolas will then have crossed each other and assumed a reverse relationship which hardly represents any true biological situation. Our mathematical devices must stay tempered with common sense.)

In certain cases, we have used also an arbitrary point $Y = -1.900$, $X = 0$. A glance at FIGURES 20 and 22 will tell why. So will the values of A in entries 5, 6, 7, 16, 19, 23 of TABLE 26: we want a value of A close to these, but preferably slightly less, arithmetically, than any or most of them. (In TABLE 26, the least reliable formulae thereby are 13, 15, 18.)

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* The references to "formulae" under this heading are those of TABLE 26.

The formulae, then, appearing in TABLE 26 are derived mostly from the same assembly of mammalian data as before, with occasional supplementing from von Bonin. In each case, there have had to be at least 2 genera (*e.g.*, the extinct ungulates from TABLE 13) so spaced that the parabola obtained from them would not be grotesque in comparison with the rest. In certain cases, notably that of the rodents, and perhaps also the Cetacea, the results have seemed grotesque to me anyway (although the rodents are well represented—see TABLE 14), but it would be a biased procedure to omit them. Even if the genera be spaced at good intervals, there is no assurance of fitness in their parabolas. Unless the genera are represented by something like their mean or type values, they will be misleading. If an order is being formulated, the few genera that stand for it may be atypical of the order; that is, in a fuller representation of the order, perhaps they lie at some distance from the true line of mean tendency for the order. Also, it is more difficult to obtain a satisfactory parabola, if the members of the order are all small. If, in addition, their correlation of body and brain weight be poor—a trait that appears to hold among small-bodied orders more than among large-bodied—again the result may be badly "off." This apparent fact may be important, evolutionally; for good results in geometric statistics, it is vitiating.

Once these deterrents are recognized, we may yet find that the aggregate of the evidence points in a certain direction. Hence its use.

The Stocks Severally

Proboscidea. Crile and Quiring give data of 1 male *Heterohyrax*, whence

log brain weight = 1.0888,
log body weight = 2.8751.

If we make an average from 2 Indian elephants (from Brummelkamp, see our TABLE 13), then average that quantity with Crile and Quiring's 1 African elephant, we obtain for the genus:

log brain weight = 3.7031
log body weight = 6.6628.

The use of the hyracoid at the critical mid-range of the parabola is very risky. So, in TABLE 26, formula 12 uses the two points above, plus the shrews, and formula 13 uses ($Y = -1.900$, $x = 0$) the shrews and the elephants, but not the hyrax.

Perissodactyls. There are plenty of horse data in Crile and Quiring. But the horse is a domesticated animal: the body appears to me exaggerated with respect to the brain, when it is compared with the zebra and the rhinoceros. Unfortunately, I have no data on the Przewalski. But the zebra data are good. (Incidentally, the zebra ontogenetic curve comes very close indeed to that of the domesticated horse.) While TABLE 13 has supplied reconstructions of two *Mesohippi*, their use would have given a parabola so very flat as compared with that of the Pecora and Carnivora, and it would have lain so far away from these, that it has not seemed best to place reliance on the reconstructed values of two *Mesohippus* specimens.* The perissodactyls have been formulated twice (formulae 14 and 15), using in both cases the zebras, the rhinoceroses, and the shrews.

Cetacea. In Crile and Quiring's work, and in von Bonin's collection, there are data for the genera *Phocaena*, *Delphinapterus*, *Lagenorrhinchus*, *Tursiops*, *Globiocephalus*, *Megaptera*, and *Balaenoptera*. Von Bonin considers the latter two genera as unusable, because of an excess amount of fat, so he calculates his rectilinear regression without them. Just at what point one should stop and say, "From such a body weight on, the animals all have too much inanimate weight to be considered," I cannot say. The problem presents itself whenever we have a sample population of mature animals, such as monkeys, or man, where body weight continues to increase long after cessation of brain growth, or where a digestive tract may be heavily loaded. As another instance, Crile and Quiring's adult horses are mostly old animals (as well as domesticated), hence unusable. Anyway, to return to the Cetacea: formula 21 includes all the whales, taken at face value.

The result is that the values of b and c are both extraordinarily high. The isauxon point is far above that of all other mammalian stocks except the primate. This may be the actual situation, but it obviously must be suspect. The curvature of the parabola may have two defects: the lesser whales, which are placed close to the human proportion of brain/body weight, may by that token be immature specimens; the great whales, by reason of much blubber, may be unduly weighted the opposite way. The result would be a high-arching, rapidly down-curving parabola. So, a reassessment (formula 22) includes only the great whales, the shrews, and the now familiar point ($Y = -1.900, X = 0$). Perhaps the true state of affairs is intermediate to formulations 21 and 22.

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* There are several similar instances, where a genus or other division places a little too far to the right and not high enough for the rest of a series: *Hyrax*, *Tragulina*, Viverridae, Lemuroidea on the whole; as far as existing evidence goes. Further data in these and other cases are very desirable.

Pinnipedia. These include all genera available, plus the point of the shrews.

Edentates, Chiroptera, Amblypods, Anoplotheres. As with the Cetacea, Proboscidea, and the Perissodactyla, the point ($Y = -1.900, x = 0$) is assumed. The positions of *Coryphodon* and *Uintatherium* (FIGURE 20) necessitates the use further of the shrew point. In the case of the other three, the parabolas curve close to the shrew point, anyway.

Rodents. These are a special problem. The smaller forms are close to the shrews in body size, yet the brains are larger. In fact, the mice may be even smaller-bodied, yet their brains may be at least as large. Whether the rodent order has had a peculiar and unique morphological evolution behind it or not, at least its proximity to the insectivores on a log-log chart does not tolerate passing a parabola through the shrews, as we have done with orders farther removed in size. Furthermore, we encounter again the phenomenon which seems to allow wide variation in brain weight per body weight among the small mammals. Thus, the Myoidea (FIGURE 14, entries 21–32) trend roughly along a straight-line slope of .56, but scatter widely at the lower-left end of the constellation. This can hardly be altogether an error in weighing tiny brains, for the edentates and marsupials also show low correlation between brain and body weight (see FIGURE 14). This means that we must either omit the rodents from any statistical manipulation that treats the other orders as samples of a series or a population, or else we must include them and consider their discrepancy as a sampling-error, like any other in a given set of data. There is a third possible procedure. Since, in other mammalian orders, we have usually been dealing with only limited parts, a family or a superfamily, etc., we may extract a family or a superfamily of rodents and treat them to a formulation. Whatever we do, we may be sure that the limited character of our data will allow us but a rough picture of what the situation is or has been among these animals. Accordingly, I have evaluated the rodents (formula 8) by the usual method of taking the means of their genera and using these for a mean-squares parabola. The result does not look good. Then the Sciuridae have been formulated separately, this time passing the line through the shrews. The sciurid value for A still is somewhat "off," when compared with the other mammalian lines, but until much more is known about all the stocks, particularly about their variance, this approximation will have to suffice. At least, FIGURE 23 shows that either formula places the point (b, c) in line with the others.

Marsupials. In no formula summarizing the mammals have we used any but Eutheria. The formulae of the marsupials, therefore, bear comparison with those for the "mammals." Taking all genera, from von Bonin's and our own assemblies together, we obtain a mean-squares parabola (formula 2) that is very flat and more nearly of a shape with that expressing von Bonin's Eutherian data (formula 4). If, on the other hand, we use as one datum the point $(Y = -1.900, X = 0)$ as before, we obtain formula 3. As for how close to the shrews the parabola of either formula passes: when $X = 1.24$, formula 2 gives $Y = -.374$ and formula 3 gives $Y = -.610$; the shrew value being $Y = -.4597$, which is intermediate.

2. The Correlative Behavior of the Constants *b* and *c* in the Mammalian Parabolas

a. The Formula Relating c and b

Consider FIGURE 23 and TABLE 26.

In spite of the various degrees of independence between bodies of data (nothing could be more independent than the reptilian from the mammalian), *all* the points in FIGURE 23, which are the plots of c against b, follow very closely a straight-line tendency. Note that the reptiles are in consistent agreement. (In FIGURE 23A, the scales of b and c are equal, while in FIGURE 23B, the c-scale has been exaggerated 10 times.) So close do the points all come to lying on a straight line, that it hardly matters what procedure we adopt for formulating that line. Of the several possibilities, here are four:

(1) By using the same 10 mammalian parabolas that have yielded formula 6, TABLE 26:

$$c = f(b) = .0697 - .118b.$$

(2) By using the same 10 mammalian parabolas that have yielded formula 7, TABLE 26:

$$c = f(b) = .0884 - .1335b.$$

(3) By using the values of c and b from the reptile parabola (1, TABLE 26) and the mammalian values of c and b in formula 5, TABLE 26:

$$c = f(b) = .0784 - .115b.$$

(4) By using the same reptilian values, and the mammalian of formula 7, TABLE 26:

$$c = f(b) = .0842 - .1305b.$$

The range in slope in these four is from —.115 to —.1336. Their arc tans. range from approx. —6° 34′ to —7° 36′, a difference of a little over 1°.

Notice that the slopes in the formula using the reptilian point (the third and fourth) do not differentiate themselves from those using mammalian values only (the first and second).

For the correlation coefficient of b, c see later.

It is striking to see the reptilian point according with a line determined from the formulae of extant mammals only, and to see that the Anopletheria and Amblypoda (points 17 and 18) likewise seem to accord. The lack of other similar points forbids pushing the speculation farther. If, however, other data should some day make of the present (b, c) formulation a more widely applicable generalization, then indeed we should be close to some phylogenetic law.

ADDENDUM

A NOTE ON THE RELIABILITY OF A POSITIVE CURVATURE TO THE REPTILIAN PARABOLA

On an earlier occasion (see Section E 1), we doubted that a parabola of plus-curvature truly represented the reptilian morphology. We speculated that the Crocodilia might well occupy an exceptionally high position in their class, after the positional analogy (let us say) of the primates among the mammals. Perhaps we are now in a better position to test the crocodilian trajectory.

If we examine the lower-left region of the reptilian constellation (FIGURE 20), we find a cluster of amphibians and reptiles, including the mean point of 15 *Lacertae*. Still farther to the left are several scattered specimens, R 11, A 10, A 12, respectively, Little Gecko, *Hyla arborea*, *Alytes obstetricus*. Very little reflection is needed to conclude that no matter how tiny in body we may suppose any reptile ever to have been, the brain weight could not have been much lower than this region: that is, we cannot imagine a curve coming up to the region under scrutiny from some region far below it on the Y-scale. Even fishes (see Brummelkamp, 1939) would not locate far down vertically below the region of R 11, etc. Therefore, we can hardly be far wrong in imagining the ancestral crocodilian trajectory passing through this general region.

Now, if we may invoke the equations relating c to b, and choose the point of the 15 *Lacertae* (R 4 on the figure) as an at all safe, even if rough, proportion for the ancient crocodilian ancestors, and take the average values of brain and of body weight for the five *Crocodili* in TABLE 21, we have the following equations:

$$Y = A + bX + cX^2$$

$$-.91721 = A + 1.69897b + 2.8865c \text{ (15 \textit{Lacertae})}$$

$$1.05308 = A + 5.12931b + 26.310c \text{ (5 \textit{Crocodili})}$$

and

$$c = .0842 - .1305b;$$

whence,

$$Y = -1.1538 - .0046X + .0848X^2.^*$$

The indication is, therefore, that we cannot pass from the Lacertae proportions to those of the Crocodilia, by way of a parabola having a negative *c*-value, without doing violence to a reasonable set of proportions between brain and body weight for the crocodilian phylum. In which case, the concept of an increase in *proportion* of log brain-weight as log body weight increases, in at least some reptiles, seems strengthened.

b. Notes on the Degree of Independence between the Constants c and b

When points tend to cluster along a single line (as we have had other occasion to remark), that line tells of a correlation between two variables. Any tendency to diverge to either side of that line (experimental error aside) may be looked upon as bespeaking a degree of non-correlation between the two. Since the points of FIGURE 23 do not lie perfectly on one straight line, the question is in order whether the deviations are those of experimental error only, or whether the several mammalian stocks actually do, or did, tend to vary a little in the ratio between *b* and *c*.

To some extent, the error must indeed be one of samplings and of the assumptions made in deriving the formulae. Yet the deviations, I believe, must also be to some extent real, and not just statistical, error. For instance, the anoplotheres and the extant ruminants actually lie in different places in the mammalian constellation. And from FIGURE 23, it appears that they are not far apart in their values of *b*, but that the anoplotheres had a larger numerical value of *c*. (In fact, this raises the question of whether, in closely related animals like these extinct and extant ruminants, this may not be the scheme by which they are related and by which they differ. Naturally, it is still impossible to answer the question.)

From the theoretical standpoint, or speaking ideally, there is no reason why what now appears on FIGURE 23 as a sporadic distribution of points, should not once have been somehow more regular, and much more populous. That is, it were imaginable that Nature experimented within limits suggested by FIGURE 23, with all or many possible combinations of b and c. While we cannot know whether this really happened or not, the constellation in the figure certainly represents a fragmentation, for very many mammalian lines are now extinct. Of the ruminants, there has been more than one stock-line, but only one (main trend) remains. The situation being what it is, it is useless to ask whether, if we had all stock lines ever produced by the class Mammalia, the mean of them would coincide with the present mean or not. The position of the edentates, amblypods, and anoplotheres suggests that, by recent time, the line of means had shifted somewhat to the right. But whether the shift has maintained the same slope or has changed it, cannot be answered now.

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* Y is a minimum at $X = .0271$. The line is always ascendant over the stretch embraced by empirical data.

For the present, we must note carefully that the points on the diagram are quite independent of size of brain and body. The primate point, for instance, belongs to the Cercopithecidae quite as well as to *Homo*. This is illustrated by FIGURE 22, where a sample number of the cephalization exponents is drawn.

We now have the four rules:

1. If b is large and c is small, the parabola will be very steep and its curvature gradual;
2. If b is large and c is large, the parabola will start steeply but will curve more rapidly;
3. If b is small and c is small, the parabola will start at a low angle and will curve gradually;
4. If b is small and c is large, the parabola will start at a very low angle and will curve rapidly.

3. The Correlation Coefficient

Empirically, the relation of c to b has been found almost, but not quite, constant.

Now, the points of FIGURE 23 have very unequal value, so that we cannot obtain an unbiased correlation coefficient. Admitting the handicap, and using the points at their face value, we may compute a correlation. Almost the *poorest* correlation possible would use from TABLE 26 the formulae 1, 2, 4, 8, 10, 11, 12, 14, 16, 17–21, 23, which render:

$$r_{bc} = -.912.$$

A theoretical system of cephalization coefficients, in which

$$r = -1.000,$$

is always possible. Whether it would have empirical backing, or whether the latitude allowed by an imperfect correlation represents something biological, is, of course, impossible to say.[*]

G. THE STATISTICAL ANATOMY OF THE MAMMALIAN CLASS (Concluded)

ON THE POSITION OF THE CONSTANT *A* IN THE CEPHALIZATION EXPONENT

1. The constant A in the cephalization exponents has been the value of Y where $X = 0$. This is true, also, in the formula $Y = A + bX$. The Dubois school has called antilog A, which is a in $y = ax^b$ (to use our own terms), the cephalization coefficient.

The scale of a or A is as arbitrary as Fahrenheit or Centigrade, since there is no significant biological point at $X = 0$ (or $x = 1$).

In a previous heading, we have found the intersection between the reptilian and a mammalian parabola. It would be more substantial, biologically, to take such a point as the origin of all mammalian parabolas, even though this mathematical quantity is sharper than the biological event it seeks to locate.

With some such fixed point, it becomes possible to symbolize, in imagination, the rise of the mammalian curves out of the reptilian in this fashion:

Let the reptilian parabola be a flexible steel rod, secured at the calculated point of intersection with the mammalian parabola. Then apply a lifting-force to it, close to the fixed point, and also a weight. Gradually increase the upward pull, and at the same time slide the weight farther to the right.

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[*] Assume that $r = -1.000$ and calculate a cephalization exponent for *Simia* by assuming only the empirical means Y, X for *Simia* and for *Blarina*, and any one of the formulae $c = f(b)$. Repeat, replacing *Simia* with *Homo*. Imagine, then, a time when the (common?) ancestors of man and of orang had the general proportions of Cercopithecidae. It does not matter whether one pretend that the ancestors had already differentiated towards their descendants or whether they were still an unidentifiable portion of the cercopithecid magma. In either case, there could have been statistically a variation in brain weight percentage. The variation is present even today, and it is wide. Next, take some convenient cercopithecid body weight—say, the mean. Calculate Y for this mean for the cephalization exponents of *Homo* and of *Simia*. None of the empirical formulae $c = f(b)$ listed in Section F 2a can be made to give values of c and b such that calculated Y's for mean cercopithecid X do justice to the respective exponents and yet fall within the range of cercopithecid brain weights for that body weight.

1. Assume: $c = .0842 - .1305\ b$; then,
Simia: $Y = -2.2443 + 1.5918\ X - .1234\ X^2$
Homo: $Y = -3.0338 + 2.359\ X - .2238\ X^2$
Let $X = 3.3021$; then, from
Simia: $Y = 1.6677$; antilog $= 46.5$ gm.
Homo: $Y = 2.3162$; antilog $= 207.1$ gm.

2. Assume: $c = .0697 - .118\ b$; then
Simia: $Y = -2.1059 + 1.4625\ X - .1028\ X^2$
Homo: $Y = -2.7331 + 2.042\ X - .1711\ X^2$
Let $X = 3.3021$; then from
Simia: $Y = 1.1671$; antilog $= 14.7$ gm.
Homo: $Y = 2.1499$; antilog $= 141+$ gm.

Such conflicting results do not, of course, disprove the possibility of $r_{bc} = -1.000$. However, pending future corrections which may so indicate, it is best to assume the correlation is not perfect. Above all, it is essential to remember the "as if" character of the cephalization exponents.

At every point except where it is fixed, the steel rod will rise, its inclination will steepen, and the curvature will become sharper. Its behavior resembles that of a fishing-rod after a "strike."

In analytical geometry, this behavior is a "transformation."

As a working case, let us transform the reptilian parabola into several of the mammalian of TABLE 26: entries 9, 16, 19, 20, 23, and the general mammalian to which they contributed, 7.

1. The fixed point, the point of intersection of reptilian and mammalian lines, is for entries 1 and 7, TABLE 26:

$$Y = -1.6217$$
$$X = .2385.$$

The point is now the origin of a new set of axes:

$$Y' = 0,\ X' = 0. \quad \text{Then,}$$
$$Y' = Y + 1.6217$$
$$X' = X - .2385.$$

The six mammalian parabolas are to be corrected, or "warped," to pass through this point.

This may be done as follows: Take arbitrary values of X, and calculate Y for each; rewrite X and Y in terms of X' and Y'; form the new equations $Y' = 0 + b'X' + c'X'^2$; and solve for b' and c'. The results are in TABLE 27.

A comparison of TABLES 26 and 27 will show that the "corrections" have not been severe. For instance, if we calculate primate values of Y'. X' from TABLE 27 and derive from them values of Y, X, we obtain TABLE 28.

Two profitable operations now follow in the next two sections.

2. The vertical distances between the reptilian parabola and any mammalian are given by:

$$Y' \text{ (mammal)} - Y' \text{ (reptile)} = (b'X' - c'X'^2)_M - (b'X' + c'X'^2)_R.$$

Rewriting the two sides of the equation,

$$RY = mX' - nX'^2.$$

Interpreted back into the antilogarithms, it reads

$$\frac{y' \text{ (mammal)}}{y' \text{ (reptile)}} = \frac{\text{antilog } (b'X' - c'X'^2)_M}{\text{antilog } (b'X' + c'X'^2)_R}.$$

Writing the ratio of the y's as ry,

$$ry = \frac{x'^m}{x'^{2n}}.$$

See TABLE 29 for the values of RY.

The regularity of the family of curves suggests that m and n are correlated. (With the Dubois formulation, this could not happen, since all slopes are parallel.) The ratio of n to m is a very good straight line for Sciuridae, Pecora, Carnivora; Pinnipedia: $n = -.05413 - .0773\ m$; *Homo* deviates. In this scheme (it has not seemed worth illustrating by a graph), the "lowly-brained" Sciuridae are placed at the left end of the line, the "higher-brained" to the right, with *Homo* leading, followed by the Pinnipedia and then by the Carnivora and Pecora simultaneously. The line $RY = mX' - nX'^2$ is a parabola giving 0 values where the mammalian cephalization exponents intersect the reptilian, and giving a maximum value where

$$X'\ (\textit{mutatis mutandis},\ X) = \frac{b_M - b_R}{2c_M + 2c_R}.$$

TABLE 30 gives these maxima twice: once as calculated by using TABLE 26, once by taking the first derivatives of the formulae in TABLE 27. In the latter case, the point X' so found has to be reinterpreted into $X = X' + .2385$. It will be seen that agreements are very close, again indicating that no great violence has been done by bending all curves to pass through a common point on the reptilian line.

These values of X' happen to occur in the most populous portion of the mammalian constellation (see FIGURE 20), where (except for Primates) body weight ranges around 6–10 kg. The value of X' in the primate line happens to occur where man is located. Whether these are accidents and devoid of significance, I cannot say.

3. The transformation now resolves itself. The X' axis remains unaltered, but the mammalian lines have come about by a change of *slope* λ from the reptilian. This is a one-dimensional strain: a transformation in the Y'-dimension only. Then

$$\lambda\ (\text{mammal}) = l \times \lambda\ (\text{reptile})$$

$$\frac{\lambda\ (\text{mammal})}{\lambda\ (\text{reptile})} = l.$$

Since $$\lambda = \frac{dY'}{dX'} = b' + 2c'X', \text{ we have}$$

$$l = \frac{b' + 2c'X'\ (\text{mammal})}{b' + 2c'X'\ (\text{reptile})}.$$

The curves of empirical l are formulated in TABLE 31.* Notice that l is always great for small values of X', and falls off (parabolically) as X' increases. That is, the distortion or transformation takes place most strongly where the mammals are smallest of body.

A clue to quantitative understanding of evolutional changes in body shape, as well as in the matter of brain/body ratio, lies in the geometry of transformations. D'Arcy Thompson (1942, pp. 1051 *et seq.* The material is present also in the first edition) has depicted it graphically for the skull and the body shapes of certain animals. He has presented a challenge to the students of human evolution which, some day, must be met in terms of a kinetic somatometry.

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* The high arithmetic values of the constants in the pinniped formula may indicate a faulty reconstruction of its original cephalization exponent.

FINALE

There appears to be nothing aberrant about the rise of man, no need to search for some *tertium quid* by which a whimsical Nature struck off at a new tangent to produce a cerebration which caricatures that of the mammalian rank and file. That *tertium quid* does not exist. In fact, if one is looking for a really great upsurging of cephalization, one should contemplate the long and steep rise (of the logarithms) from Reptilia to Insectivora, or the lesser, yet still enormous, achievement from Insectivora to Hapalidae. Compared with these, the rise from monkey to man is the smaller biological achievement. Let us not confuse standards. The *practical results* that come from the exercise of the aggregate human brain, the combined efforts of humans which we term "culture," certainly are spectacular when compared with the analogous achievements of other animals. However, in the world of biological operations, especially when scaled in its intima by logarithms, the abysmal discrepancy does not exist.

As for the word "aberrant," if one feels he must use the term at all, when speaking of mammals, it were well first to be sure just what is meant by it.

SECTION IV

ONTOGENY AND COMPARATIVE ANATOMY

A. PRIMATES

Consider FIGURE 24.

The two fetal human and the fetal *Semnopithecus* curves of TABLE 12, plus their mean (see SECTION III, 3); the postinfantile curves for man, orang, chimpanzee, *Semnopithecus,* and *Rhesus,* from TABLE 11; the exponent of cephalization from the shrew-monkey-man line; and the adult means of species from TABLE 16, are all plotted.

It will be recalled that the comparative-anatomic line was constructed on the assumption of mean values for shrews, for Cercopithecidae minus the baboons, and a heterogeneous congeries of 41 humans.

1. The chart shows a marked parallelism between the fetal lines, derived from an absolutely different mass of data, and the comparative-anatomic, over a considerable stretch. The lower ends of the two lines diverge, and perhaps we shall recall the suggestion that it is apparently before our data come in that the embryo has pushed up its brain weight to a size greater than that of a putative adult ancestor of corresponding body weight. The embryo has appropriated a larger percentage of its growth-energy to the brain.

2. Most, but not all, of the adult monkeys cluster about the comparative-anatomic line. This, of course, is by hypothesis. The exceptions are an interesting assortment: the great apes, the gibbons, the *Rhesus* macaque (according to Zuckerman and Fischer, but contrary to Spitzka), most of the Prosimiae. The variability of body weight is responsible, but far less so that of brain weight. Some of this variation may have positive significance, some of it may not. Thus, there can be no doubt about the placement of the great apes; the several species of gibbon corroborate each other; so do the lemurs. The Cercopithecidae, on the other hand, are uncertain because of the macaque contradiction. We have the ontogenetic data for *Semnopithecus* and *Rhesus,* which certainly do not permit pushing these forms back among the clustered means of other Cercopithecidae. We could probably fill out the interval between them all if we had more data. (Some, but by no means all, of the adults are marked as emaciated. Spitzka was very careful

to annotate his juveniles, and so were Hrdlicka and Crile and Quiring. Thus, the safest procedure was, as noted before, to use the means of the aggregate adults.)

We remark again that the baboons, as well as the Hapalidae of Hrdlicka and of Crile and Quiring, immediately align themselves on this same curve. Interestingly enough, from the standpoint of the assumption that the smaller members of a stock should be the more conservative, so does that minute prosimian, *Microcebus minimus* (to judge from the single specimen listed by von Bonin). So, taken altogether, it seems a not unfair conclusion that the *Homo* line is not unrepresentative of the rise of the Primates, and that there is a phyletic tendency to push out to larger body size, once a certain brain level has been reached, without much further increase in log brain weight.

At any rate, it is very doubtful if any fetal lines of monkeys would lie above and to the left of the human fetal line, since that would give them, shortly before birth, a brain size larger than that of a human fetus of equal body weight, but of far less advanced morphology. This should make the human fetal line a limit of an area; the postnatal growth of the monkeys must take place between it and the point where their adult forms are registered. If they all should have postinfantile slopes of the general range between *Semnopithecus* and male *Rhesus* (within this range have occurred all animals we have dealt with, except man and the anthropoids), then we may form rough ideas of where the several monkey forms would have their fetal development.

3. The human ontogenetic line turns out approximately parallel to the primate line. Measured in terms of logarithmic cycles, the horizontal distance between the two lines is approximately uniform over a large part of the inscribed area. Man actually travels a very short horizontal distance from the fetal slope to his position on the line of pseudo-phylogeny. So do some monkeys. Apes travel a very long distance. So do large baboons, like *Hamadryas*. These forms I would term "giants," at their level of brain size.

B. PRIMATES AND OTHER MAMMALS

1. A. H. Hersh (1941, p. 138) publishes a diagram furnished him by B. G. Anderson, which is a "hypothetical logarithmic plot intended to illustrate ontogenetic and evolutionary relative growth and the way in which they may be related to each other." I had already been working on FIGURE 29 when this diagram came my way, and I was struck by the coincidences. Hersh's diagram has a set of steep ontogenetic lines which take a sharp turn to the right by reducing their slopes, and an-

other, a "phylogenetic" set, which start with low slope and turn abruptly upward at much increased slopes. The two sets of lines, therefore, inevitably intersect. In case of the lines developed as a system in the present essay, a phylogenetic claim is not being made for them, as we have been careful to state. None the less, the similarity of scheme or structural system cannot but be noticed.

About the lower ends of my own curves, nothing but surmises could be offered. But, at least after the data begin, the upward sweep of both sets of lines is clear enough. My empirical lines differ from Hersh's hypotheticals in certain regards: his are mainly rectilinear; my comparative-anatomic lines are parabolas (because of the *c*-factor); and my fetal lines are plotted as straight lines only, as the best approximation it is safe as yet to make. In the matter of brain and body weight, I am not willing to stress the "law of allometry" as strongly as is done by Hersh. Nevertheless, we seem to agree on something more fundamental than a mere formula.

2. In FIGURE 24, I have confined the representation to three orders: Primates, Carnivora, Artiodactyla. On the fetal side, the Carnivora are represented only by the (domestic) cat.

I trust I court no misunderstandings in assembling these materials.

The artiodactyls are represented, on the fetal side, by the Bovidae of Section II; on the postnatal side, by the antelopes of Section III.

It is noticeable that the domestic forms—cat, sheep, ox—reach adult size below the comparative-anatomic lines.

The crosses are plots from the line of mean mammalian, comparative-anatomic trend.

How far the ontogenetic lines parallel the comparative-anatomic, can be seen at a glance. At their lower ends, the ontogenetic trail off markedly from any parallelism, but we cannot say whether they should continue (in the backward direction) to trail off, or whether they should dip again.

Another striking feature is the very small interval between an ontogenetic line for Carnivora or Pecora and the comparative-anatomic, as contrasted with the very wide interval of the Primates. This ties in with the much more gradual slopes, both ontogenetic and comparative-anatomic, of the less cephalized orders. Without that coincidence, there is no geometric reason why the cat or ox fetal curve should not lie as far from the comparative-anatomic curve, during its earlier career anyway, as in the case of the Primates. But what would be the consequence? A fetal specimen with a far huger brain than it actually possesses, but an adult brain of the size actually obtaining.*

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* Analogous to speeding very quickly towards a destination, then slowing down to a crawl in order not to arrive too soon.

3. The small squares on the diagram indicate the spot where, in the pertinent formulae of TABLE 26, the slope is 45°: *i.e.*, the point of isauxon. Before that spot is reached, the log brain weight is increasing faster than the log body weight. It was to have been expected that, for the mammalian cephalization to ascend out of the reptilian, the log brain weight would gain over the log body weight. The situation, as we have seen, boils down to this:

(a) The log brain weight usually ceases to gain over the log body weight, somewhere in the neighborhood of the Insectivora. By token of the analysis in Section III F, the exponent with the lowest value of b and of c (numerically) will reach isauxon the earliest. The Primates owe their preeminence to a particularly advantageous ratio of b to c; although, in principle, there is nothing peculiar about this ratio.

(b) Nevertheless, cerebral complexity continues to increase, as we know. But it does seem reasonable that the "set" of these parabolic directions was a necessary prelude or prerequisite to the evolution of high cerebral "capacity."

(c) The primate fetal curve stands off at a far greater elevation from the comparative-anatomic than in the other orders. Both curves are steeper than those of other orders. This double steepness must be ontogenetic and comparative-anatomic aspects of fundamentally one and the same thing.

(d) It may be that primate species are far more prone to vary in cephalization than the other orders. This point would, at least, be consistent with the preceding ones.

4. What has now happened to the "*exposant de relation*" and the "*coefficient de céphalisation*" of Dubois *et al.?* The criticisms of von Bonin (that the premises on which they are based are now archaic), seem quite justified. Yet von Bonin, I believe, went too far when he jettisoned the promise of dynamic implications below the face of his chart. The concept of a "progressive cephalization," I am convinced, is real. This shines through Dubois' exponent and coefficient. It persists in the issues underlying Brummelkamp's illustrations which we have reproduced in this study. This is despite of what I feel to be a fact: namely, that the sloping staff of straight parallel lines in those illustrations really extract just about what they first put in. Repeatedly, we have seen the slopes of the parabolas, in their mid-regions, ranging their values in the neighborhood of .56. In those limited reaches, then, the cephalization coefficient still remains as a handy rule-of-thumb for comparing the relative heights of several lines of cephaliza-

tion. That the cephalization exponent herein set forth comes, as I really believe, closer to describing the situation than does the *exposant de relation* and the *coefficient de céphalisation,* in no wise alters my conviction that Dubois' first "cracking" of a very important problem is a landmark in the progress of biology.

ADDENDUM

Since finishing this paper, an old reference in my card catalogue has turned up. It is a quotation from M. Boule, *"La Paléontologie Humaine en Angleterre,"* p. 67: *"Un jour viendra où l'on découvrira un Hominien de petite taille, à la station à peu près droite, à la boîte cérébrale relativement très volumineuse par rapport au volume total du corps, mais très inférieure, en valeur absolue, à celle de tous les Hominiens déjà connus. Ce sera le véritable* Eoanthropus."

SECTION V

A. SUMMARY

1. In man and other mammals, relative increase in brain and body weights, in ontogeny, has three periods after the embryo has become a fetus: (a) a fetal, measurable as a *first approximation* by $y = ax^b$, or $\log y = \log a + b \log x$, where y is brain weight, x is body weight, in grams; (b) a postinfantile, measurable in like terms, but with a far higher $\log a$ value and far lower b value; (c) a transitional period between them, starting at an indefinable point before birth and ending indefinably in the postinfantile period. This third period is an adjustment between the two others, and in its logarithmic form is curvilinear. The first derivatives of the rectilinear formulae under (a) and (b) form upper and lower asymptotes, to which the first derivative of (c) is an asymmetric logistic:

$$\frac{d(\log y)}{d(\log x)} = \frac{K}{1 + \epsilon^v} + d,$$

where d is the lower asymptote, K is the difference between upper and lower asymptotes, and $v = f\ (\log x)$, which is expressed fairly as a third-degree parabola. However, as far as can be ascertained,

$$\int \left[\left(\frac{K}{1 + \epsilon^v} \right) d(\log x) \right]$$

is unobtainable. Hence, the integral curve remains a matter for mechanical methods.

Quantitatively, the sexes in man never behave alike throughout growth.

The comparative behavior of man, other primates, and certain ungulates, carnivores, *et al.* has been sufficiently summarized in Section IV B. It will be seen there that the differences of behavior lie in the values of the constants. However, "first approximation" (above) has been used advisedly, since the fetal curves perhaps are straight lines only in a general way. More accurately, they may fit some as yet unformulated parabolae of not less than third degree, or some other undulant curves. If so, it is logical to standardize them for comparisons, by way of a common scale of logarithmic cycles.

2. On the side of comparative anatomy, evidence is presented for

an *exponent of cephalization,* by which route a line of mammals may be considered progressively to have raised its brain weight y in proportion to its total body weight x: where $Y = \log y$, $A = \log a$, $X = \log x$,

$$Y = A + bX - cX^2,$$

$$y = ax^{b - c\log x}.$$

The last formula, it is considered, is more correct in the present case than any form $y = ax^b$, which by various authors has been applied as the "law of allometric growth" to many different biological phenomena. It means that we should write, not:

$$\frac{dY}{dX} = b, \qquad \text{but:}$$

$$\frac{dY}{dX} = b - 2cX,$$

$$\frac{d^2Y}{dX^2} = -2c,$$

in which c is an important term. By analogy, $2c$ is compared to the gravitation constant g; except that c is a variable, which is therefore analyzed further (see 3, below).

The formula is at variance with that of Dubois, which, in the symbolism above, would read $y = ax^{.56}$, the latter being the basis for saying that, when two different but related species or genera of whatever body weight have equal values of a, they may be joined by a line $Y = A + bX$, where $b = .56$.

While agreeing with some of von Bonin's criticism of Dubois, the parabolic formula above does not agree with von Bonin's conclusion that regression of log brain weight on log body weight for the Mammalia taken as a whole is rectilinear. The reasons for the disagreement are given.

As a secondary matter, the conclusion of Lapicque, that different-sized strains or individuals within a species may be arranged along a logarithmic diagonal of slope ranging to either side of .25, so that this quantity may be taken as standard, is not justified by the present study. The variations on either side of that figure are characteristic of the data used in each case, and cannot be dismissed. That adults within a species tend to orient along an axis of a positive slope that is steeper than that of the mass tendency in growth of the species, is just another phenomenon of variance in a species. It does not justify such artificialities built upon it as the Index of Cerebral Value of Anthony and Coupin.

3. The anatomy of the relationship between b and c is as follows:

$$c = f(b), \text{ and is rectilinear (see FIGURE 23);}$$

$$r_{bc} = -.912.$$

Therefore, a system exists by which may be obtained a set of second-degree parabolas, each parabola being the cephalization exponent for a given evolutionary line of mammals, as stated above.

The set, as a whole, has a parabola of mean tendency, and an expressible variance for each constant in the formula. Thus, each parabola of the set can be measured absolutely and relatively for its deviation from a central norm.

The text explains:

(a) TABLE 26, which lists 23 second-degree parabolic cephalization exponents, covering the Reptilia as a class, the Mammalia as a class, and various mammalian evolutionary stock-lines (see FIGURE 22).

(b) The variance along the straight line, $c = f(b)$, is constant, in that the errors on either side of that mean are about the same over its entire ascertained length. This variance may be measured on a line intersecting $c = f(b)$ at any point and normal to it.

4. By a very slight correction in the curvature of the parabolas which does no significant violence to the data, they can all be warped to pass through a common point of intersection with the reptilian parabola. Thereby, it becomes possible to shift the axes so that this point shall be the origin. This makes it possible to measure at all points the vertical difference between any mammalian line and the reptilian; and, further, to calculate the transformation of slope from the reptilian to that of any mammalian order. This is done by considering the elevation from the reptilian parabola to the mammalian as a distortion of ordinate. The ratio between the slope of a mammalian parabola and the reptilian is a second-degree parabola.

In retrospect, the author is aware that many criticisms can be leveled at the steps of this development. The data are not too abundant; their sources are varied and not subject to uniform control; the shrews are made to bear the weight, it seems, of the entire mammalian class; sometimes much is made out of little, etc. Of course, it is too late now to apologize. This study has not been written for the individual who contends that one has a right to open his mouth only after the mass of data has reached overwhelming proportions.

As for the numerical validity of the several formulae, quite probably every single one of them will be subject to correction when more material becomes available. As they stand, I think they are good enough to demonstrate a certain regularity of behavior of all mammals, including man.

Another weakness remains. We have postulated an exponent that is a parabola of the second degree. We have not disproved the fitness of some other curve that is concave downward. We have gone ahead to the dissection of the *b* and *c* constants, as though they had been definitely established as entities. I think it is true, nevertheless, that the configurations shown in FIGURE 22 support them as a working hypothesis, for the curvatures of the various lines are the most abrupt for the highest lines, pointing to zeniths reached the soonest. Certainly, also, the tie-in of the reptiles that has been suggested at least makes for a system. The adoption of the second-degree parabola has had a certain logic of the immediate. Hitherto, authors have exploited the formula (quite as empirically determined as our own, and with far less analysis to back it), $y = ax^{.56}$ or $Y = A + .56X$. It is quite definitely true that such lines demand a negative correction-term, if they are to fit a more lengthy range of data. It lies immediately at hand, therefore, to try $- cX^2$. The results have been good, but, admittedly, our approach has the weakness of its strength: it is purely empirical. I fail to see how it could be otherwise; nevertheless, there is much to be done before the hypothesis becomes secure.

However, it can hardly be denied that extant animals can be related to each other by some such curves as we have demonstrated. It is also undeniable that the larger-bodied animals budget a smaller percentage of their total weight-producing growth energy to brain than do the smaller animals. The curvatures that run between or through them must be concave downward. In brief, I have more confidence in the scheme of principles set forth herein than in any of the concrete numbers that have served to bring them out.

B. CONCLUSIONS

Ontogeny

1. In man and in other mammals, the growth of brain weight with respect to body weight has three periods: a fetal period, a transitional period through infancy, and a period thence to adulthood.

(In the following, all quantities are referred to in terms of their logarithms.)

2. In most of the fetal period, the growth plots approximately a straight line. In life after infancy, it plots another straight line. The first is steep and the second very gradual. Between the two is a period shown by a curving line that joins them.

3. Whatever be the meaning of this, it is during the time of curvi-

linear growth that mitoses of brain cells diminish to none, so that growth of brain material, thereafter, occurs only by enlargement of cells.

4. The sexes do not coincide exactly at any point.

5. When man is compared with some other primates, and the comparison is then broadened to include some ungulates and certain others, it appears that:

(a) In fetal life, the primates have, on the average, steeper slopes of growth than the artiodactyls. But steepness of slope in the fetal period cannot be equated simply with greater adult brain, since the pigs have the steepest slope of the artiodactyls used, and it may be as steep as the human and steeper than the monkey's. But man's line also is steeper than the monkey's, probably on a par with that of the chimpanzee. Superiority in brain size is partly traceable back to the prefetal period.

(b) In postinfantile life, the rise of brain weight, relative to body weight, is less in man than in the monkey. Other mammals resemble the monkey in this respect, except for the anthropoid apes, which distinctly belong with man. In fact, they surpass man in having a *still lower* rise of brain weight relative to body weight.

The artiodactyls differ as much intramurally in their prenatal slopes as the primates. After infancy, the primates are variable as just described, while the artiodactyls (with but small difference in brain organization) are very uniform.

6. The human brain, during the measurable fetal period, does not grow much more rapidly than the monkey's. There are two reasons for the preponderance of the human brain:

(a) *Before* the measurable period, it has already achieved a larger proportionate size. After that, it maintains its lead by but little more than pacing the monkey rate.

(b) More important, the preponderance is in terms of a steeper increase in body and brain taken together with respect to morphological levels of maturation. Thus, when the monkey is ready to be born, the human body of the same log weight and only slightly greater log brain weight is still unready for birth. Growth continues for some time thereafter, at a rate which approximately had been followed by both man and monkey. Brain preponderance demands large absolute body size.

7. In man and in other mammals, the adults of different sizes do not arrange themselves at all as though they were merely cessations of growth at various points along the line of mean tendency for the group.

Thus, small adults do not appear like "arrested adolescents," nor large ones as "overgrown" along the same line. This interpretation is at variance with that of Lapicque, who first pointed out the phenomenon.

Comparative Anatomy

8. Phyletic increase in complexity of cerebral organization (its character is not necessary to the discussion) requires phyletic increase in absolute brain size. That increase is contingent upon phyletic increase in total body size, quite as certainly as in the matter of ontogenetic increase.

9. The phyletic increase of brain size, concomitant with that of body size, does not follow the system developed by Eugène Dubois and his followers. On a log-log chart, that system would be a mass of straight lines having an average slope of .56. Instead, the logarithm of brain weight traces against the logarithm of body weight an ascending curve, concave on the lower side.

Along this curve occur the various-sized and variously evolved extant families and genera of the order. Such a curve is expressible as a second-degree parabola.

This parabola is the "exponent of cephalization." The principle applies to individual orders or to the general trend among extant mammals as a class. The parabolas behave so as to rise and disperse from a common center in the region of the insectivores.

10. The exponents of cephalization are not random in their constants: there is a clear system of relationship between them. This system has a number of formulable features.

11. The reptilian cephalization exponent is an ascending parabola, concave on its upper side. The constants in its formula fit, nevertheless, into the relational scheme that answers for the mammals.

12. The mammals have arisen from very small reptiles by a formulable step-up in the proportion of body weight devoted to brain.

13. However, the mammalian step-up is largely confined to those portions of brain practically unrepresented in the reptiles. There seems to be no great discrepancy between the reptilian brain/body weight ratio on the one hand, and on the other, the ratio between body weight and the roughly homologous portion of brain in the mammal, when the mammal is equivalent to the reptile in body size.

14. In the total mammalian system of parabolas, the steepest is that primate line which leads to man. But there is nothing at all unique about it; man is not aberrant. His blueprint, so to speak, was in-

herent at the time when some primitive animals became mammals, just as the blueprints of all other mammals were inherent. In fact, from cercopithecid to *Homo* is less of a stadium than that from hapalid to cebid or from insectivore to hapalid.

15. When, finally, ontogenetic growth and comparative-anatomy lines are compared, as far back as the former can be traced in the materials at hand, a certain parallelism exists between fetus and comparative anatomy. The fetal line, however, tops the comparative-anatomic, in such a way that a fetus of a given body size always has a heavier brain than some extant adult relative of equal body size, who presumably is less evolved. In the primates, this preponderance is much greater than in any other line. Since, in all this discussion, the ratios are those of a part of the whole, it means that, when one weighs an assortment of mammalian fetuses, for any particular and equal body weight, the primate has put more material into the weight of brain than has any other mammal. And the shapes of the various curves indicate that fetal preponderance starts much farther back in the embryonic life than the measurements extend. After birth, the ontogenetic line has no comparative-anatomic implications now discernible.

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TABLES 1-31

TABLE 1

BRAIN WEIGHTS AND BODY WEIGHTS OF HUMAN FETUSES

Michaelis, 1906			Various authors				
Age, lunar months	Av. Brain weight, gm.	Av. Body weight, gm.	Age, months	Av. Brain weight, gm.	Av. Body weight, gm.	Number (*total—185*)	Author
I	.....	2.8	4	19	138	1	G
III	4.0	17.5	4	47.3	363	3 ♀	R
IV	12.5	73.2	5	26	188	1	G
V	38.5	300.0	5	58.2	435	6 ♂	R
VI	80.4	553.6	5	58.9	428	5 ♀	R
VII	109.5	797.0	6	95.2	561	7 ♂	R
VIII	146.0	1286.0	6	87.0	623	1 ♀	R
IX	275.0	1994.0	7	108	920	1	G
			7	140.1	1061	5 ♂	R
			7	124.0	1104	7 ♀	R
			7	185.5	1175.7	30 ♂	CM
			7	184.1	1219.7	35 ♀	CM
			8	229.7	1525	2 ♂	R
			8	256.8	1764	34 ♂	CM
			8	274.81	1857	47 ♀	CM

G: Giese; R: Rüdinger; CM: Cruikshank & Miller.

TABLE 2

CHIMPANZEE

Particulars	Brain wt., gm.	Body wt., gm.	Author
♀ Premature birth	* 96	770	Coupin, *fide* A
♂ Premature birth	*270	2377	Anthony & Coupin
♂ Premature birth	*318	5490	S
♀ Premature birth	*302	5560	S
♂ 3 years	340	5500	Weber, *fide* A
♂ 3 years	347	5500	Möller, *fide* A
♂	348	6115	Weber, *fide* A
2—3 years	362	6540	Möller, *fide* A
1½—2 years	379	7430	Embleton, *fide* A
♂ 2—3 years	*412	7500	Marshall, *fide* A
4 years	381	9000	Bischoff, *fide* A
♂ 4 years	379	9400	Anthony & Coupin
4 years	367	9760	Möller, *fide* A
♀ 4 years	365	12000	A
♂ 4 years	376	14200	A
♀ 4 years	*316	16060	Anthony & Coupin
Over 4 years	391	16650	Möller, *fide* A
Over 4 years	375	19252	Owen, *fide* A
Over 4 years	376	19290	Owen, *fide* A
Over 4 years	345	21090	Meyer & Bischoff, *fide* A
♂ Over 4 years	430.5	25850	CQ
♀ Over 4 years	325	43990	CQ
♂ Over 4 years	440	56690	CQ

A: Anthony, 1928; CQ: Crile & Quiring; S: Spitzka, 1903.
* Omitted in calculating the postinfantile formula.

TABLE 3

ORANGUTAN

Particulars	Brain wt., gm.	Body wt., gm.	Author
♀ complete milk dentition	*248	3170	Keith, *fide* A
♂ young	334.5	5925	Weber, *fide* A
♂ young	339	8830	Weber, *fide* A
♂ 1st molar in use	340.2	7600	Rolleston, *fide* A
♂	365	7500	Manouvrier, *fide* A
♂ young	375	11275	Weber, *fide* A
♂ 4½ years, in captivity	325.1	18600	Owen, *fide* A
♀ young	*306	20200	Weber, *fide* A
♂ adult	400	73500	Deniker & Boulart, *fide* A
♂	395	76500	Fick, *fide* A
♂	326	72575	H
♂	347.5	49895	H
♂	359	86183	H
♂	368	63503	H
♂	371	54431	H
♂	384	83915	H
♂	395	90720	H
♂	422	79379	H
♀	*267	34474	Oppenheim, *fide* H
♀	*274.5	36287	H
♀	*279	35834	H
♀	*283	36288	H
♀	*287.5	44452	H
♀	*291	34019	H
♀	*304	36741	H
♀	*322	32659	H
♀	*326	32659	H
♀	*340.5	39917	H
♀	*344	37195	H

A: Anthony, 1928; H: Hrdlicka, 1925.

* Omitted in calculating the postinfantile formula. Adult males were averaged, and the unweighted mean used.

TABLE 4

SEMNOPITHECUS

S. maurus, fetuses (Hulshoff Pol, *fide* Anthony, 1928)			*S. obscurus*, postnatals (Keith, 1895; also, Keith, in Anthony, 1928)		
Particulars	Brain wt., gm.	Body wt., gm.	Particulars	Brain wt., gm.	Body wt., gm.
	2	20	♀ about birth	42.8	514
	3	21	♂ complete milk dentition	62.8	2730
	9	64	♀ 1st premolar in use	57.8	2520
	12	112	♀ 2nd premolar erupting	65	3170
	21	168	♂ last canine & molar unerupted	64.4	3230
	21	172	♂ same	60.5	3630
	22	189	♂ 3 adults	67.8	6540
	24	255	♀ 7 adults	62.8	5045
	25	322			
	26	341			
	30	251			
	30	255			
New-born	32	390			
New-born	32	392			

TABLE 5

DOMESTIC CAT

Particulars	Brain wt., gm.	Body wt., gm.	Author
12-cm. fetus	* 2.3	65.8	Keith & Mies, *fide* Z
♀ new-born	* 6.5	122	Keith & Mies, *fide* Z
3 hours	* 4.8	105.6	Keith & Mies, *fide* Z
2 days	* 5.1	124	Keith & Mies, *fide* Z
4 days	* 6.7	162.7	Keith & Mies, *fide* Z
8 days	* 8	206.3	Keith & Mies, *fide* Z
♂ 10 days	* 9	207	A
♂ 10 days	* 9	222	A
♂ "young"	*16.1	338	Weber, *fide* A
♀	*21	490	A
♀ 2 months ca.	21	600	A
♀ 2½ months	22.5	701	Weber, *fide* A
♂ "young"	26	990	A
♀ 3½ months	26.5	1220	Weber, *fide* A
♂ "young"	24	1442	A
♂	28	1888	A
♂ "young"!	27	2350	A
♂ 6 months ca.	30	2500	A
♂ 7 months	28	3045	A
♂ 5 adults	*31	3300	Weber, *fide* A

A: Anthony, 1928; Z: Ziehen, 1906.
* Not used in the calculations.

TABLE 6

SHEEP

Fetuses (Ziehen, 1906)		Postnatals (Crile & Quiring, 1940)		
Brain wt., gm.	Body wt., gm.	Brain wt., gm.	Body wt., gm.	Number
2.5	57.5	* 73.6	6870	8
3.61	60.0	* 71.5	8550	5
3.36	68.3	88.6	15760	4
3.75	68.0	109	40230	9
4.43	98.0	106.5	52100	7
5.07	127.2			
5.34	114.7			
5.23	131.7			
5.79	121.0			
5.84	154.0			
8.33	182.3			
8.15	173.5			
7.65	208			
8.67	242.4			
10.02	273.5			
12.01	369			
15.2	480			
19.8	666			
17.35	571			

* Not used in calculating the postinfantile formula.

TABLE 7

Ox

Fetuses (Ziehen, 1906)		Postnatals (Crile & Quiring, 1940; steers omitted)		
Brain wt., gm.	Body wt., gm.	Brain wt., gm.	Body wt., gm.	Number
1.72	28.55	*193.9	19500	1
2.37	43.85	*215.2	22000	1
3.21	55.9	304	51900	3 ♂
4.83	91.4	299	90000	6 ♂
5.72	159	356	214000	5 ♂
6.91	174.5	386	241000	3 ♂
9.23	349	384	367000	2 ♂
11.94	384	*357	371000	7 ♀
9.72	393	*408	412000	213 ♂
15.31	559	*408	413000	218 ♀
16.45	746	*403	450000	62 ♀
		*473.5	489900	1 ♀
		*417	491000	44 ♀
		*420	506000	71 ♀
		*408	552000	5 ♂
		*415	574000	200 ♀
		*444	591000	2 ♂
		*447	597000	10 ♂
		*471	861000	2 ♂
		*462	888000	5 ♂

* Omitted from the calculation of the postinfantile formula.

TABLE 8

FETAL PIG

(Pooled data of Anthony, 1928, and Ziehen, 1906. Anthony's source: L. G. Lowry.)

Number	Brain wt., gm.	Body wt., gm.	Author
3	.02	.29	A
5	.06	.70	A
6	.10	1.70	A
5	.19	3.25	A
2	.34	4.97	A
6	.69	10.33	A
4	1.37	28.20	A
1	1.11	42.50	Z
1	1.68	45.00	Z
1	2.35	56.10	Z
10	2.00	63.54	A
1	2.55	72.60	Z
4	2.47	74.90	A
1	2.54	77.50	Z
1	2.45	76.00	Z
1	2.45	76.50	Z
1	2.61	77.50	Z
1	2.35	78.00	Z
8	3.20	90.20	A
3	3.86	97.00	A
1	2.50	100.00	Z
1	2.60	105.50	Z
22	5.10	126.45	A
3	6.22	153.00	A
6	6.88	216.50	A
1	8.13	283.00	Z
5	10.25	288.80	A
5	11.01	334.70	A
5	13.78	395.00	A
3	18.97	465.00	A
1	13.83	485.00	Z
1	9.26	535.00	Z
5	25.21	731.00	A
3	29.50	745.00	A
1	33.04	826.00	A
1	30.85	858.00	Z
1	34.45	1352.00	Z

TABLE 9

HORSE

(*Crile & Quiring, 1940; geldings omitted.*)

Number	Average age	Brain wt., gm.	Body wt., gm.
Fetuses			
3 ♀	91 days, premature	183.3	13000
1 ♀	71 days, premature	226	19500
5 ♀	46.4 days, premature	254.4	26470
5 ♂	54.4 days, premature	273.9	27300
1 ♀	60 days, premature	ca. 242	31750
11 ♀	14.6 days, premature	333.9	47680
15 ♂	16 days, premature	317.3	38910
Infants			
19 ♀	5.6 days old	366.5	54320
18 ♂	3.1 days old	370.1	52450
1 ♂	3 months old	400	92980
3 ♂	33.5 days old	425.3	93890
4 ♀	83 days old	470.2	116770
1 ♀	3 months old	475	118800
Postinfantile, but immature (only this category used in calculating formula)			
1 ♀	6-7 months old	492	181400
2 ♀	1 year old	525	184160
8 ♂	9 months old	582.8	285130
2 ♂	1 year old	588	300500
5 ♂	1 year old	602.4	306350
2 ♀	1 year old	616	380110
7 ♀	2-3 years old	632	408500
3 ♂	2-3 years old	621.4	433920
Adults			
21 ♂ ♀		520	230900
31 ♀	14 years	468	262000
1 ♂	30 years	573	362800
1 ♂		504	362870
1 ♀	18 years	604	376480
1 ♀	25 years	692	380750
1 ♀	15 years	690	402650
10 ♀	19.1 years	637.7	443360
1 ♂	27 years	618	461760
5 ♂	17.2 years	706.7	485310
1 ♀	12 years	655	521640

TABLE 10

PROSPECTUS OF THE FORMULAE FOR POSTINFANTILE AND FOR FETAL PERIODS

Genus		Postinfantile	Fetal
1. *Homo*	♂	X	X
	♀	X	
2. *Pan*	♂ ♀	X	
3. *Simia*	♂	X	
4. *Rhesus*	♂	X	
	♀	X	
5. *Semnopithecus*	♂ ♀	X	X
6. *Felis*	♂ ♀	X	
7. *Mus*	♂	X	
	♀	X	
8. *Ovis*	♂ ♀	X	X
9. *Bos*	♂	X	
	♂ ♀		X
	♀		
10. *Sus*	♂ ♀		X
11. *Equus*	♂ ♀	X	

TABLE 11

GROWTH OF BRAIN WEIGHT/BODY WEIGHT AFTER INFANCY

Genus		Number	$\log y = \log a + b \log x$	$y = ax^b$
1. *Homo*	♂	89	$2.8431 + .06326 \log x$	$696.8x^{.06326}$
	♀	62	$2.7711 + .07010 \log x$	$590.37x^{.07010}$
2. *Pan*	♂ ♀	17	$2.408 + .0389 \log x$	$255.9x^{.0389}$
3. *Simia*	♂	16	$2.4204 + .0322 \log x$	$263.3x^{.0322}$
4. *Rhesus*	♂	36	$1.2346 + .19626 \log x$	$17.163x^{.19626}$
	♀	40	$1.384 + .1449 \log x$	$24.21x^{.1449}$
5. *Semnopithecus*	♂ ♀	16	$1.4316 + .1019 \log x$	$27.01x^{.1019}$
6. *Felis dom.*	♂ ♀	10	$.8331 + .1835 \log x$	$6.809x^{.1835}$
7. *Mus norv.*	♂	211	$-.0998 + .1838 \log x$	$.7944x^{.1838}$
	♀	261	$-.1231 + .1926 \log x$	$.7533x^{.1926}$
8. *Ovis ar.*	♂ ♀	20	$1.1505 + .189 \log x$	$14.14x^{.189}$
9. *Bos taur.*	♂	19	$1.5678 + .1868 \log x$	$36.966x^{.1868}$
11. *Equus cab.*	♂ ♀	30	$1.672 + .1997 \log x$	$46.98x^{.1997}$

TABLE 12

PRENATAL GROWTH OF BRAIN WEIGHT/BODY WEIGHT

	Number	$\log y = \log a + b \log x$	$y = ax^b$	Body wt., gm. (*Approx.*,	Brain wt., gm. *at birth*)	Ratio of brain wt./ body wt.
1. *Homo* ♂ ♀ Composite data Michaelis' means	185 ?	$-.86306 + 1.0098 \log x$ $-.606 + .914 \log x$	$.13707x^{1.0098}$ $.2477x^{.914}$	3200	351*	.11
5. *Semnopithecus* ♂ ♀	14	$-.557 + .8075 \log x$	$.2773x^{.8075}$	391**	32**	.08
8. *Ovis* ♂ ♀	19	$-.885 + .774 \log x$	$.1300x^{.774}$	3400***	52***	.015
9. *Bos* ♂	11	$-.661 + .655 \log x$	$.2183x^{.655}$	20000	205	.010
10. *Sus* ♂ ♀	130	$-1.22885 + .9112 \log x$	$.05904x^{.9112}$	1450 826***	32 34***	.022 .041

* Boyd, 1942; ** Hulshoff Pol, *fide* Anthony, 1928; *** Harris, 1929.

TABLE 13

ADULT UNGULATES

(*Table 1 from Brummelkamp, 1939c; adapted.*)

Entry No.	Genus and species	Brain wt., gm.	Body wt., gm.	Ceph. coeff.
1	*Elephas indicus*	4717	3048000	1.184
2	*Elephas indicus*	4048	2047000	1.234
3	*Camelus dromedarius*	762	400000	.589
4	*Giraffa camelopardalis*	680	529000	.450
5	*Equus caballus*	532	368000	.431
6	*Alces americanus*	407	272000	.390
7	*Equus asinus*	385	175000	.470
8	*Oryx beisa*	280	107000	.450
9	*Antilope caäma*	269	99500	.451
10	*Antilocapra americanus*	130.2	34474	.393
11	*Antilope cervicapra*	90	13500	.457
12	*Gazella*	216	68000	.446
13	*Gazella isabella*	81.6	12170	.440
14	*Ovis tragelaphus*	209	56000	.481
15	*Ovis aries*	140	55000	.326
16	*Ovis aries*	94.5	28000	.320
17	*Sus scrofa (wild)*	178	56000	.410
18	*Sus scrofa* Berkshire	125	104000	.204
19	*Sus scrofa* Middlewhite	125	104000	.204
20	*Sus scrofa* ("Edelschwein" ♀)	168	281000	.158
21	*Sus scrofa domestica*	113	150000	.151
22	*Sus scrofa domestica*	90.94	104000	.148
23	*Cervus elaphus*	411	125530	.605
24	*Cervus dama*	224.5	37195	.649
25	*Cervus muntjak*	125	16600	.566
26	*Cervus porcinus*	142	30000	.462
27	*Cervus hippelaphus*	229	73500	.454
28	*Cervus capreolus*	97.5	14500	.475
29	*Rupicapra rupicapra*	118.5	26500	.414
30	*Cephalophus maxwelli*	41.1	3780	.424
31	*Cephalophus maxwelli*	38	3357	.417
32	*Cephalophus maxwelli*	37.5	3130	.429
33	*Cephalophus maxwelli*	35.4	3160	.403
34	*Damaliscus lunatus*	324	82000	.603
35	*Hippopotamus amphibius*	582	1755000	.198
36	*Bos taurus* Monthéliard	493	660000	.288
37	*Bos taurus* Vendée	480	540000	.314
38	*Bos taurus*	423	465000	.301
39	*Tapirus indicus*	265	201000	.300
40	*Tapirus americanus*	169	160000	.217
41	*Capreolus caprea*	103.5	15422	.489
42	*Capreolus caprea*	98	15000	.469
43	*Capreolus caprea*	93	14062	.461
44	*Phacochoerus africanus*	132.5	67000	.276
45	*Tayassu tajac*	101	19618	.416
46	*Tragulus napu*	18.3	2670	.228
47	*Tragulus memmina*	17.1	2368	.229
48	*Tragulus javanicus*	15.85	2037	.230
49	*Mesohippus bairdi*	88	27000	.303
50	*Mesohippus bairdi*	63	15000	.301
51	*Palaeosypos leidyi*	102	380000	.081
52	*Anoplotherium commune*	71	200000	.080
53	*Moeritherium*	173	336000	.147
54	*Diplobune bavaricum*	47.5	38500	.135
55	*Uintatherium mirabile*	150	2000000	.047
56	*Coryphodon hamatum*	44	235000	.045

TABLE 14

ADULT RODENTS

(Table 1 from Brummelkamp, 1939b; adapted.)

Entry No.	Genus and species	Brain wt., gm.	Body wt., gm.	Ceph. coeff.
1	*Hydrochaerus capybara*	75	28500	.251
2	*Dasyprocta agouti*	20	2684	.249
3	*Sciurus rufiventer*	9.2	650	.252
4	*Sciurus rufiventer*	8.95	580	.261
5	*Sciurus carolinensis*	7.58	469	.249
6	*Sciurus carolinensis*	7.48	466	.246
7	*Sciurus vulgaris*	6.10	323	.246
8	*Sciurus vulgaris*	5.81	287	.250
9	*Sciurus hudsonicus*	4.103	159	.240
10	*Hystrix*	37.5	15000	.179
11	*Lepus timidus*	16.7	3833	.171
12	*Lepus cuniculus* dom. gem.	11.20	3375	.123
13	*Lepus cuniculus* (average)	9.3	1226	.179
14	*Oryctolagus cuniculus ferus*	10.4	1440	.183
15	*Pteromys nitidus*	11.8	1600	.196
16	*Cavia cobaya*	4.73	700	.124
17	*Cavia porcellus*	4.54	675	.122
18	*Dipus hirtipes*	1.85	73	.171
19	*Sciuropterus volans*	1.92	64	.190
20	*Lagostomus trichodactylus*	8.8	3854	.089
21	*Arvicola agrestis*	.9	42.5	.112
22	*Arvicola terrestris*	.355	90.25	.027
23	*Mus agrarius*	.20	33.3	.028
24	*Mus norvegicus*	2.36	448	.077
25	*Mus rattus*	1.59	200	.084
26	*Mus musculus*	.43	20.85	.078
27	*Mus musculus*	.36	16	.077
28	*Mus sylvaticus*	.59	21.6	.107
29	"Japanese mouse"	.35	7.85	.111
30	*Cricetulus griseus*	.628	23.18	.109
31	*Mus musculus*	.475	24.32	.080
32	*Mus wagneri*	.424	18.92	.082

TABLE 15

ADULT CARNIVORES

Entry No.	Genus and species	Number	Brain wt., gm.	Body wt., gm.	Author
	Viverridae, Hyenidae				
1	*Genetta tigrina*	3 ♂ ♀	15.71	1376.3	CQ
2	*Ichneumia albic.*	1 ♂	28.30	4400	CQ
3	*Crocuta croc.*	2	175	62370	CQ
	Felidae				
4	*Felis domest.*	10 ♂ ♀	25.30	3275.6	CQ
5	*F. leo*	5 ♂	240.72	150720	CQ
6	*F. pardus*	1 ♂	135	48000	CQ
7	*F. oregonensis*	1 ♂	106.7	28790	CQ
8	*F. bangsi*	1 ♂	129	25960	CQ
9	*F. onca*	1 ♀	147	34470	CQ
10	*F. capnesis*	3 ♂ ♀	57.687	7197.7	CQ
11	*F. tigris*	2 ♂ ♀	263.5	184500	CQ
12	*F. ocreata*	1 ♀	28.48	2700	CQ
32	*F. pardalis*	2 ♂	63.1	9525.5	H
33	*F. concolor*	1 ♂	154	54432	H
34	*F. cacomistli*	1 ♀	41.9	2722	H
35	*F. serval*	1 ♂	54.1	11340	H
36	*Lynx canad.*	1 ♂	69.5	14969	H
37	*Lynx rufus*	1 ♂	65.0	6350	H
	Procyonidae				
14	*Potos flavus*	1 ♀	31.05	2620	CQ
15	*Procyon lotor*	4 ♂ ♀	39.19	4288.25	CQ
38	*Nasua rufa*	1 ♀	34.0	3175	H
39	*Potos caudiv.*	1 ♀	35.1	1863	H
	Canidae				
16	*Vulpes lagopus*	1 ♂	44.50	3385	CQ
17	*Vulpes fulva*	1 ♀	53.30	4625	CQ
18	*Urocyon ciner.*	1 ♂	37.28	3749	CQ
19	*Otocyon megal.*	1 ♀	26.09	3335	CQ
20	*Thos mesomelas*	2 ♂	46.00	2850	CQ
21	*Canis latrans*	1 ♀	84.24	8510	CQ
22	*C. familiaris*	9 ♂ ♀	78.945	13404.4	CQ
23	*C. familiaris*	1 ♂	105.9	24490	CQ
24	*C. familiaris*	3 ♂	113.57	30146.7	CQ
25	*C. familiaris*	6 ♂ ♀	87.287	25423.3	CQ
26	*C. lupus*	1 ♂	119	22680	CQ
27	*C. lubilis*	1 ♂	152	29940	CQ
	Ursidae				
28	*Ursus horribilis*	1 ♀	233.9	142880	CQ
29	*Thalarctos mar.*	2 ♂ ♀	498	258285	CQ
40	*Ursus horribilis*	1 ♂	389	149688	H
41	*Ursus torquatus*	1 ♂	269	69860	H
42	*Melursus urs.*	1 ♀	267	136080	H
43	*Helarctor malay.*	1 ♀	385.5	45020	H
	Mustelidae				
30	*Mustela arctica*	4 ♂ ♀	5.0975	157.22	CQ
31	*Mephitis meph.*	3 ♂ ♀	10.10	2073.3	CQ
44	*Putorius putor*	1 ♂	7.87	915	H

CQ: Crile & Quiring; H: Hrdlicka.

TABLE 16

ADULT PRIMATES

Entry No.	Genus and species	Number	Brain wt., gm.	Body wt., gm.	Author
2	*Semnopithecus entellus*	1 ♂	117	6647	S
3	*Cercopith. sp.*	4 ♂ ♀	59.75	2469	S
4	*Cercopith. mona*	1 ♂	67	3001	S
5	*Cercopith. griseo-vir.*	1 ♂	72	3202	S
6	*Chlorocebus sab.*	1	71	1480	S
7	*Chlorocebus cynoc.*	1	68.5	3880	S
8	*Cercocebus fulig.*	2 ♂ ♀	98	1375.5	S
9	*Macacus rhes.*	24 ♂	79.94	1598.46	S
10	*Macacus rhes.*	24 ♀	78.52	1941.21	S
11	*Macacus rhes.*	7	88.57	1783.57	S
12	*Macacus cynomolg.*	4 ♂	62.5	1653.75	S
13	*Macacus cynomolg.*	5 ♀	61.2	1354.2	S
14	*Macacus nemestr.*	5 ♂	118.4	6786	S
15	*Macacus nemestr.*	3 ♀	99.33	2989	S
16	*Macacus sinus*	3 ♂	67	963.67	S
17	*Macacus pileatus*	5 ♂ ♀	63.1	1402.6	S
18	*Macacus speciosus*	1 ♂	98	5560	S
19	*Macacus melanotus*	1 ♂	80	1105	S
20	*Cynopithecus niger*	2 ♂	108	5920	S
21	*Cynocephalus bab.*	5 ♂ ♀	137.4	2541.8	S
22	*Cynocephalus hamad.*	1 ♂	199	10230	S
23	*Cynocephalus hamad.*	6 ♀	121.17	2224.17	S
24	*Cynocephalus anubis*	1 ♀	152	5000	S
25	*Cynocephalus sphinx*	1 ♀	135	2481	S
26	*Cynocephalus leucoph.*	1 ♀	124	1718	S
27	*Mycetes cavaya*	1 ♂	45	826	S
28	*Mycetes ursinus*	1 ♀	19	1025*	S
29	*Ateles beelzebus*	1 ♀	97.5	1870	S
30	*Lagothrix humb.*	1	112	4850	S
31	*Cebus capuc.*	5 ♂ ♀	70.2	1453.4	S
32	*Cebus capill.*	2 (♂)	73	1515	S
33	*Cebus hypoleuc.*	3 ♂	54.33	587	S
34	*Cebus subcrist.*	1 ♂	71	902	S
35	*Cebus albifrons*	1 ♂	58	675	S
36	*Hapale penic.*	1 ♀	8	206	S
37	*Iacchus vulg.*	8 ♂ ♀	7.81	219.75	S
38	*Midas urs.*	1 ♀	24	361	S
39	*Lemur brun.*	1 ♂	26	1505	S
40	*Nycticebus tard.*	1 ♂	12	612	S
41	*Simia satyrus*	8 ♂	371.6	72575	H
42	*Simia satyrus*	11 ♀	299.8	36439	H
43	*Hylobates sp.*	3 ♂ ♀	101.7	6125.7	H
44	*Hylobates agil.*	9 ♂	87.45	5946	H
45	*Hylobates agil.*	3 ♀	79.8	5180	H
46	*Hylobates mulleri*	3 ♂	96.8	5516	H
47	*Hylobates mulleri*	4 ♀	92.6	6348	H
48	*Symphalangus*	3 ♂ ♀	133.5	12079	H
49	*Oedipomidas*	3 ♂ ♀	9.35	305.2	H
50	*Homo*	41 ♂ ♀	1320.15	62080	CQ
51	*Leontocebus geoffroyi*	184 ♂ ♀	8.21	275.5	CQ

S: Spitzka, 1903; H: Hrdlicka, 1925; CQ: Crile & Quiring, 1940.
* Misprint?

TABLE 17

ADULTS OF OTHER EUTHERIAN ORDERS

Genus and species	Number	Brain wt., gm.	Body wt., gm.	Author
		Edentates		
Tamanduas tetradactyla	2 ♂ ♀	25	3692	CQ
Dasypus novemcinctus	10 ♂ ♀	7.5	3401	CQ
Bradypus griseus	12 ♂ ♀	15.33	3156.5	CQ
Choloepus hoffmanni	8 ♂ ♀	23.44	4880.75	CQ
		Pinnipedia		
Erignathus barabtus	1 ♀	460	281000	CQ
Odobenus rosmarus	1 ♂	1126	667000	CQ
Phoca richardi	1 ♂	442	107300	CQ
Phoca hispida	5 ♂ ♀	253	39570	CQ
Phoca vitulina	5 ♂ ♀	270.5	12610	H
		Chiroptera		
Desmodus rotundus	5 ♂ ♀	8.95	818.2	CQ
		Insectivora		
Scalopus aquaticus	1 ♂	1.16	39.6	CQ
Blarina brevicauda	68 ♂ ♀	.347	17.36	CQ
		Cetacea		
Phocaena phocaena	1 ♂	1735	142430	CQ
Delphinapterus leucas	6 ♂ ♀	2351.7	395280	CQ
Balaenoptera musculus	1	6800	58059000	CQ

CQ: Crile & Quiring, 1940; H: Hrdlicka, 1925.

TABLE 18

CRANIAL CAPACITIES OF SOME PALEANTHROPOI, AND CALCULATIONS OF BRAIN WEIGHTS

(*Hrdlicka, 1930.*)

Specimen	Volume measured by	cc.	Brain wt., gm. (*mihi*)
Ehringsdorf		1450?	1270?
Eoanthropus	Smith Woodward	1300	1139
	Elliot Smith	1200	1051
	Keith	1400	1226
Gibraltar	Sollas	1250	1095
	Keith	1200	1051
La Chapelle	Boule	1600–1626	1401–1424
La Quina	H. Martin	1350	1182
Le Moustier	Weinert	1564	1370
Neanderthal	Schaffhausen	1033	
	Huxley	1230	1077
	Schwalbe	1234	1081
Pithecanthropus	Dubois	1000+	
	Dubois	900	789*
	Weinert	1000	870–920†
Rhodesia	Elliot Smith	1280	1120
Rome	Sergi	not over 1200	ca. 1050

* Using Bolk's ranges and 900 cc., one gets 664–846 gm.

† Weinert's estimate.

TABLE 19

THE *Homo* LINE

$(Y = -2.2417 + 1.54915\ X - .0899\ X^2.)$

Groups	Empirical X	Empirical Y	Calculated Y	Source of raw data *see*
* 68 Blarinae	1.2396	−.4597	−.4597	TABLE 17
184 Hapalidae	2.4401	.9143	1.0028	TABLE 16, item 51
15 Cebidae	3.1498	1.8422	1.7458	TABLE 16, items 27, 29–35
* 93 Cercopithecidae	3.3021	1.8949	1.8928	TABLE 16, items 2–19
17 Baboons	3.4688	2.1057	2.0493	TABLE 16, items 20–26
* 41 Homines	4.7929	3.1206	3.1273	TABLE 16, item 50

* Data used for calculating the line.

TABLE 20

RELATIVE INCREASES OF CEPHALIZATION IN SOME PRIMATE STAGES, ASSUMING THE INSECTIVORES AS A BASE

Groups compared	Differences of Y	Differences of X	Ratio
Marmosets / Shrews	1.495	1.2005	1.245
Cercopithecidae / Marmosets	.8596	.8620	.996
Baboons / Cercopithecidae	.2108	.1667	1.265
Humans / Baboons	1.0149	1.3241	.767
Humans / Cercopithecidae	1.2257	1.4908	.822

TABLE 21

BRAIN AND BODY WEIGHTS, AND CEPHALIZATION COEFFICIENTS, OF SOME REPTILES

Entry No.	Number	Genus and species	Body wt., gm.	Brain wt., gm.	Ceph. coeff.
		*Crile & Quiring's Data, 1940**			
R 1	1 ♂	*Alligator miss.*	109000	8.40	.012715
	1 ♂	*Alligator miss.*	52400	7.23	.01656
	1 ♂	*Alligator miss.*	173000	11.20	.01289
	1 ♂	*Alligator miss.*	205000	14.08	.01498
	1 ♂	*Crocodilus amer.*	134000	15.60	.02109
R 2	1 ♀	Gila Monster	514	.729	.02219
R 3	1 ♀	Iguana	4190	1.44	.01353
R 4	15 ♂ ♀	*Lacerta viridis*	50	.121	.01356
R 5	3 ♂ ♀	Black Snakes	431	.291	.00977
R 6	20 ♂ ♀	*Tropidonotus*	70	.100	.00927
R 7	6 ♂ ♀	*Zamenis*	220	.209	.01022
R 8	30 ♂ ♀	*Emis*	250	.25	.01141
R 9	30 ♂ ♀	*Testudo*	320	.30	.01189
R 1		*Mean for Crocodilia*			.01565
		Mean for Ophidia			.00952
		Median of reptilian means			.01258

Entry No.	Genus and species	Body wt., gm.	Brain wt., gm.	Ceph. coeff.
	Dubois' Data, 1913†			
R 10	Monitor	7500	2.44	.0165
R 11	Little Gecko	4.7	.043	.0181
R 12	Emerald Lizard	16.8	.093	.0191
R 13	Cobra	1770	.646	.0098
R 14	Common Viper	64.2	.105	.0102
R 15	Common Lizard	12.507	.076	.0185
R 16	Slow Worm	16.252	.039	.0082
	Slow Worm	18.9	.037	.0071
R 17	Greek Tortoise	993.58	.360	.0075

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* Cephalization coefficients mine.

† Cephalization coefficients his.

Table 22

Brain and Body Weights, and Cephalization Coefficients, of some Amphibia

(*Table 1 from Brummelkamp, 1939d, adapted; his sources: Dubois, Donaldson.*)

Entry No.	Genus and species	Brain wt., gm.	Body wt., gm.	Ceph. coeff.
A 1	*Rana catesbyana*	.204	244.40	.009614
A 2	*Rana virescens*	.153	73.35	.01407
A 3	*Rana esculenta*	.1137	52.90	.01254
A 4	*Rana esculenta*	.106	44.50	.01287
A 5	*Rana esculenta*	.1007	39.21	.01312
A 6	*Rana pipiens*	.1165	44.20	.01419
A 7	*Rana temporaria*	.0909	34.80	.01265
A 8	*Rana temporaria*	.0861	31.30	.01272
A 9	*Rana fusca*	.088	53.00	.009696
A 10	*Hyla arborea*	.043	4.80	.01799
A 11	*Bufo vulgaris*	.073	44.50	.008862
A 12	*Alytes obstetricus*	.041	7.70	.01319

Table 23

Human Brain weighed by Parts; Ratio between Pons-Medulla and Encephalon

(*Data of Marshall, 1892.*)

I Number	II Ages	III Av. body wt., lbs.	IV Av. encephalon wt., ozs.	V Pons-medulla wt., ozs.	VI Ratio of V/IV
			Males		
55	20–30	92.14	47.9	.93	.0194
103	30–40	93.35	48.2	.98	.02012
135	40–50	102	47.75	1.06	.0222
110	50–60	102.5	47.44	.98	.02065
123	60–70	103.13	46.16	.97	.0210
102	70–80	106.13	45.5	.94	.02064
24	80–90	99	45.34	.89	.01961
Totals and means 652	20–90	99.75	46.88	.97	.0207
			Females		
70	20–30	86.13	43.7	.88	.0201
85	30–40	87	43.09	.91	.0211
97	40–50	84	42.81	.89	.02075
100	50–60	86	43.12	.86	.01992
142	60–70	86.14	42.69	.83	.0194
146	70–80	80.4	41.27	.88	.0213
75	80–	79.5	39.77	.82	.0206
Totals and means 715	20–	84.19	42.35	.87	.0205

TABLE 24

PROSPECTUS FOR TABLE 25

(Orders of mammals, number of genera listed, and operators for weighting the genera.)

Order	Number of genera	Weighting operator
Primates	23	1.304
Carnivora	23	1.304
Ungulata	22	1.364
Rodentia	30	1.000
Edentata	4	7.500
Pinnipedia	3	10.000
Chiroptera	4	7.500
Insectivora	5	6.000
Cetacea	2	15.000

TABLE 25

GENERA FROM PRECEDING TABLES, GROUPED ACCORDING TO LOG BODY WEIGHT

(Some genera have been split because of wide species range in log body weight.)

Group	log body wt. not more than	Genera	Mean log brain wt.	Mean log body wt.
I	1.50	*Mus, Desmodus, Rhinolophus, Vespertilio, Blarina*	−.3533	1.345
II	2.00	*Dipus, Sciuropterus, Arvicola, Mus, Tupaya, Talpa, Scalopus*	.1291	1.786
III	2.50	*Iacchus, Hapale, Oedipomidas, Mustela, Sciurus, Mus, Geomys*	.714	2.304
IV	3.00	*Mycetes, Midas, Nyctocebus, Putorius, Sciurus, Cavia, Mus, Perodipus, Pteropus, Erinaceus*	.875	2.851
V	3.50	*Cercopithecus, Cercocebus, Macacus, Cynocephalus, Ateles, Cebus, Lemur, Genetta, Potos, Thos, Mephitis, Tragulus, Dasyprocta, Lepus, Oryctolagus, Pteromys, Fiber, Bradypus*	1.43	3.326
VI	4.00	*Semnopithecus, Cynopithecus, Lagothrix, Hylobates, Ichneumia, Felis, Procyon, Vulpes, Urocyon, Otocyon, Nasua, Cephalophus, Lepus, Lagostomus, Capromys, Tamanduas, Dasypus, Choloepus*	1.437	3.740
VII	4.50	*Symphalangus, Felis, Canis, Antilope, Rupicapra, Capreolus, Tayassu, Felis, Hystrix, Hydrochaerus*	1.98	4.282
VIII	5.00	*Simia, Gorilla, Pan, Homo, Hyaena, Felis, Helarctor, Antilope, Antilocapra, Gazella, Ovis, Sus, Cervus, Damaliscus, Phoca*	2.41	4.69
IX	5.50	*Ursus, Thalarctos, Melursus, Equus, Alces, Oryx, Tapirus, Erignathus, Phocaena*	2.855	5.26
X	6.00	*Camelas, Giraffa, Odobenus, Delphinapterus*	3.218	5.70
XI	6.50	*Loxodontia, Hippopotamus*	3.208	6.32

Table 26

Exponents of Cephalization

($Y = A + bX + cX^2$.)

Group	Exponent
1. Reptiles	$-1.7095 + .3679\,X + .03613\,X^2$
2. Marsupials, all genera	$-1.2332 + .6993\,X - .00492\,X^2$
3. Marsupials, all genera plus ($Y = -1.900$, $X = 0$)	$-1.9140 + 1.1194\,X - .0679\,X^2$
4. Mammals, von Bonin's data	$-1.4045 + .8742\,X - .01363\,X^2$
5. Mammals, data of TABLE 25	$-1.8080 + 1.1540\,X - .0543\,X^2$
6. 10 mammalian "stocks" (a)	$-1.9510 + 1.3262\,X - .0871\,X^2$
7. 10 mammalian "stocks" (b)	$-1.9301 + 1.3222\,X - .0883\,X^2$
8. Rodents[3]	$-1.0146 + .6268\,X - .00141\,X^2$
9. Sciuridae[1, 4]	$-1.3835 + .9350\,X - .0449\,X^2$
10. Chiroptera[2, 3, 4]	$-1.8997 + 1.2603\,X - .0971\,X^2$
11. Edentates[2, 3, 4]	$-1.9001 + 1.3002\,X - .1112\,X^2$
12. Proboscidea[1, 3]	$-1.8069 + 1.1426\,X - .0475\,X^2$
13. Elephants[1, 2, 4]	$-1.9005 + 1.2358\,X - .0591\,X^2$
14. Perissodactyla[1, 3]	$-2.3085 + 1.6561\,X - .1333\,X^2$
15. Perissodactyla[1, 2, 4]	$-2.0840 + 1.6339\,X - .1367\,X^2$
16. Pecora (Antelopinae)[1, 3, 4]	$-1.9284 + 1.2890\,X - .0838\,X^2$
17. Anoplotheria[2]	$-1.9033 + 1.2442\,X - .1012\,X^2$
18. Amblypoda[1, 2]	$-1.9180 + 1.1818\,X - .0902\,X^2$
19. Carnivora[1, 3, 4]	$-1.9227 + 1.2830\,X - .0844\,X^2$
20. Pinnipedia[1, 3, 4]	$-2.1403 + 1.4872\,X - .1064\,X^2$
21. Cetacea[1, 3]	$-2.3473 + 1.6680\,X - .1162\,X^2$
22. Large whales[1, 2, 4]	$-1.9000 + 1.2487\,X - .0694\,X^2$
23. Primates (*Homo*)[1, 3, 4]	$-2.2417 + 1.5491\,X - .0899\,X^2$

[1] Line assumed as passing through *Blarina*.
[2] Line assumed as passing through reptilian value $Y = -1.900$, $X = 0$.
[3] Used for calculating line of 10 mammalian "stocks" (a), No. 6, above.
[4] Used for calculating line of 10 mammalian "stocks" (b), No. 7, above.

Table 27

Exponents of Cephalization

($Y' = a' + b'X' + c'X'^2$, *where the origin of the coordinate axes is taken at* $X = .2385$, $Y = -1.6217$. *Entry numbers the same as in* TABLE 26.)

Group	Exponent
1. Reptilia	$.3881\,X' + .03546\,X'^2$
7. Mammalia (modern)	$1.2799\,X' - .08841\,X'^2$
9. Sciuridae	$1.1730\,X' - .07942\,X'^2$
16. Antelopinae (Pecora)	$1.2474\,X' - .083916\,X'^2$
19. Carnivora	$1.2442\,X' - .084915\,X'^2$
20. Pinnipedia	$1.3389\,X' - .093466\,X'^2$
23. *Homo*	$1.3572\,X' - .06993\,X'^2$

TABLE 28

A CHECK ON THE *Homo* FORMULA OF TABLE 27

Group	A	B	C	D	E	F
Blarina	1.2396	1.0011	−.4597	1.1620	1.2875	1.1620
Hapale	2.4401	2.2016	1.0028	2.6245	2.6503	2.6570
Cercopithecidae	3.3021	3.0636	1.8928	3.5145	3.5018	3.5166
Baboons	3.4688	3.2303	2.0493	3.6710	3.6550	3.7274
Homo	4.7929	4.5644	3.1273	4.7490	4.7420	4.7423

A: values of X from TABLE 19.
B: $X' = X - .2385$.
C: values of Y calculated from TABLE 26.
D: $Y' = Y + 1.6217$.
E: Y' calculated from TABLE 27.
F: empirical Y from TABLE 19, plus 1.6217.

TABLE 29

THE VERTICAL DISTANCE, RY, BETWEEN A MAMMALIAN PARABOLA, $b'X' - c'X'^2$, AND A REPTILIAN, $b'X' + c'X'^2$

(*Entry numbers those of* TABLE 26.)

Group	$RY = mX' - nX'^2$.
7. Mammalia	$.8918\ X' - .12387\ X'^2$
9. Sciuridae	$.7849\ X' - .11484\ X'^2$
16. Antelopinae	$.8593\ X' - .11938\ X'^2$
19. Carnivora	$.8561\ X' - .12038\ X'^2$
20. Pinnipedia	$.9508\ X' - .12893\ X'^2$
23. *Homo*	$.9691\ X' - .10539\ X'^2$

TABLE 30

VALUES OF LOG BODY WEIGHT X, WHERE THE DIFFERENCE BETWEEN THE MAMMALIAN LOG BRAIN WEIGHT AND THAT OF A REPTILE OF EQUIVALENT BODY WEIGHT IS A MAXIMUM

(*Column A calculated from* TABLE 26; *Column B, from* TABLE 27. *Entry numbers those of* TABLE 26.)

Group	A	B
7:1 Mammalia	3.83	3.838
9:1 Sciuridae	3.49	3.648
16:1 Antelopinae	3.84	3.838
19:1 Carnivora	3.80 –	3.788
20:1 Pinnipedia	3.93	3.928
23:1 *Homo*	4.69	4.828

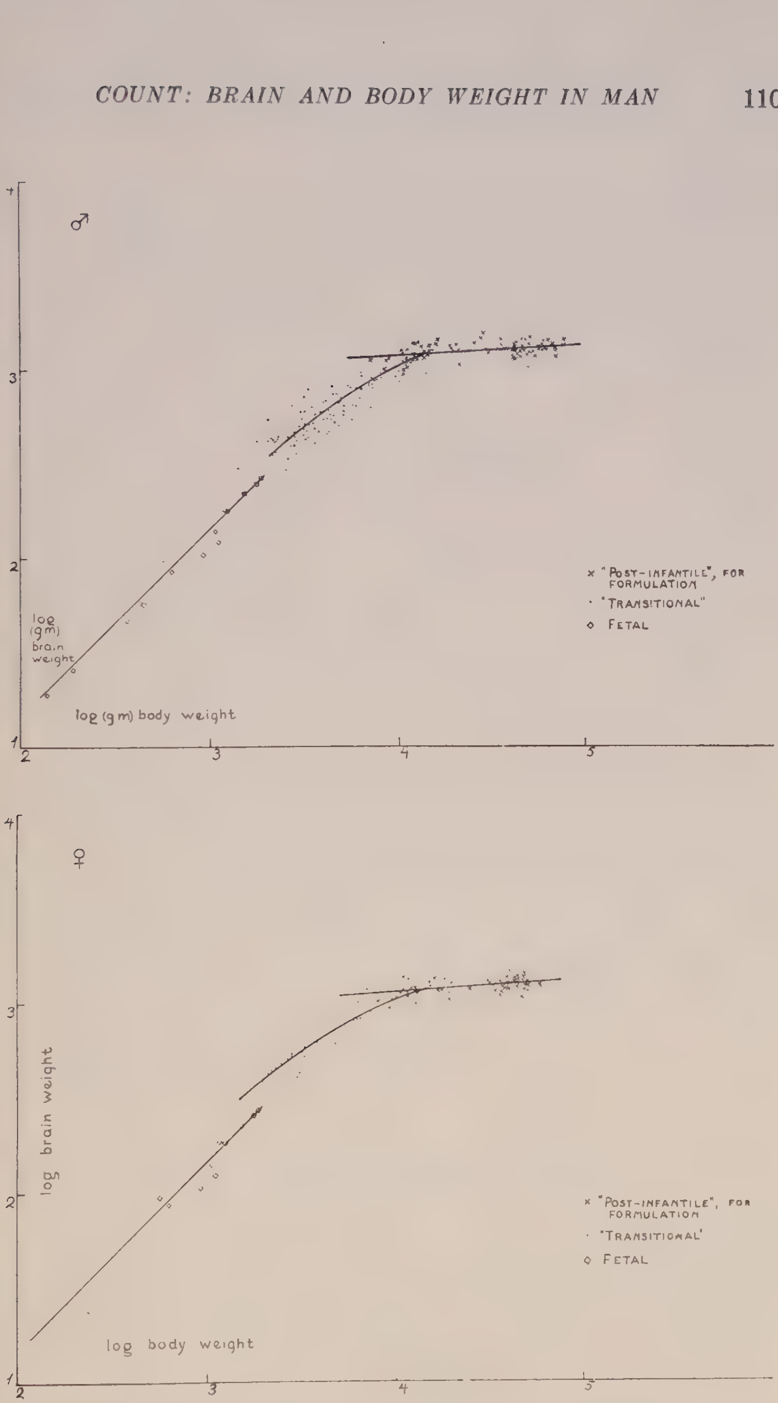
TABLE 31

VALUES OF l, WHERE $l = \frac{\lambda(\text{mammal})}{\lambda(\text{reptile})}$; λ BEING THE SLOPE OF ANY PARABOLA IN TABLE 27

(*Entry numbers those of* TABLE 26.)

7:1 Mammalia	$3.2542 - .8825\,X' + .06872\,X'^2$
9:1 Sciuridae	$3.0865 - .8010\,X' + .06212\,X'^2$
16:1 Antelopinae	$3.16897 - .8475\,X' + .06575\,X'^2$
19:1 Carnivora	$3.1653 - .8541\,X' + .06653\,X'^2$
20:1 Pinnipedia	$3.7547 - 1.1490\,X' + .10387\,X'^2$
23:1 *Homo*	$3.4492 - .8126\,X' + .05849\,X'^2$

FIGURES 1-24



FIGURES 1 and 2. Ontogeny of man, by sexes. The fetal points are means from **Michaelis** *et al.;* the dots and crosses are individuals. There is no break between dots and crosses. The categorization is by chronological age (see text), and is but a practical expedient for obtaining formulae.

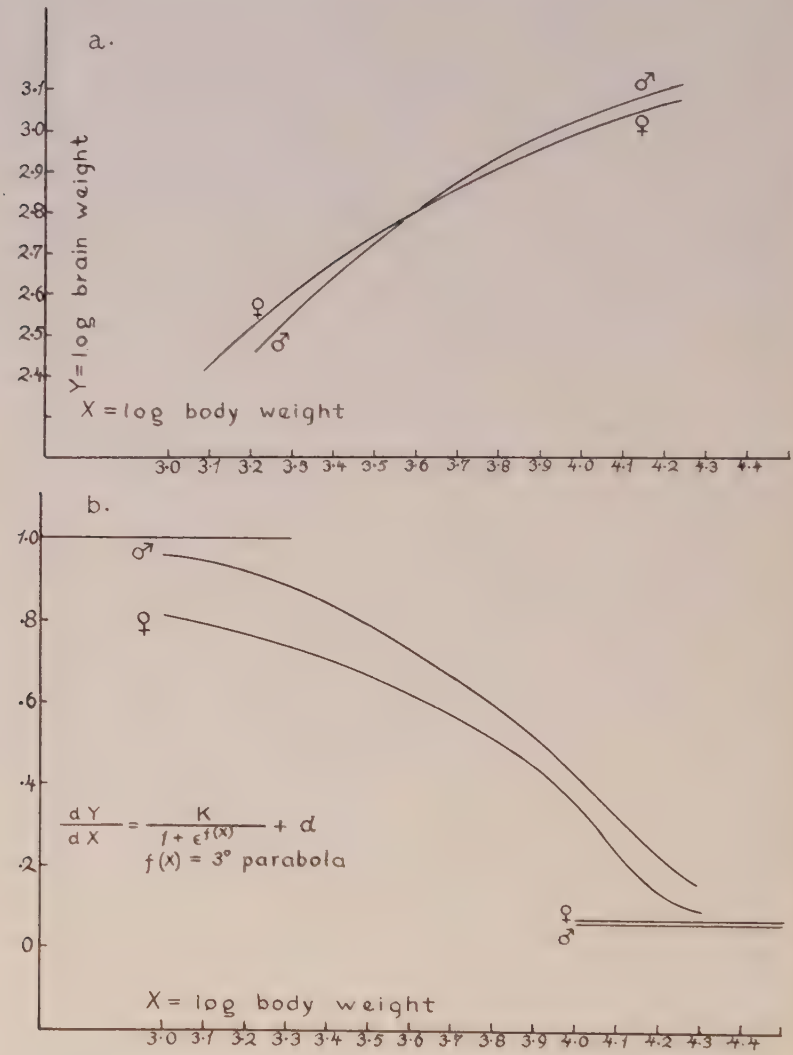


FIGURE 3. The infantile period. Detail of FIGURES 1 and 2.

a. The transitional curve between late fetus and post-infant. The curves are considered as the integrals of those drawn in b.

b. Skew logistic growth velocities. There is only one upper asymptote, because separating the sexes in the fetal period was impracticable from the data. The upper asymptote is therefore the fetal common mean growth velocity. The lower asymptote represents the velocities of the post-infantile period. The asymptotes are the derivatives of the straight lines of FIGURES 1 and 2.

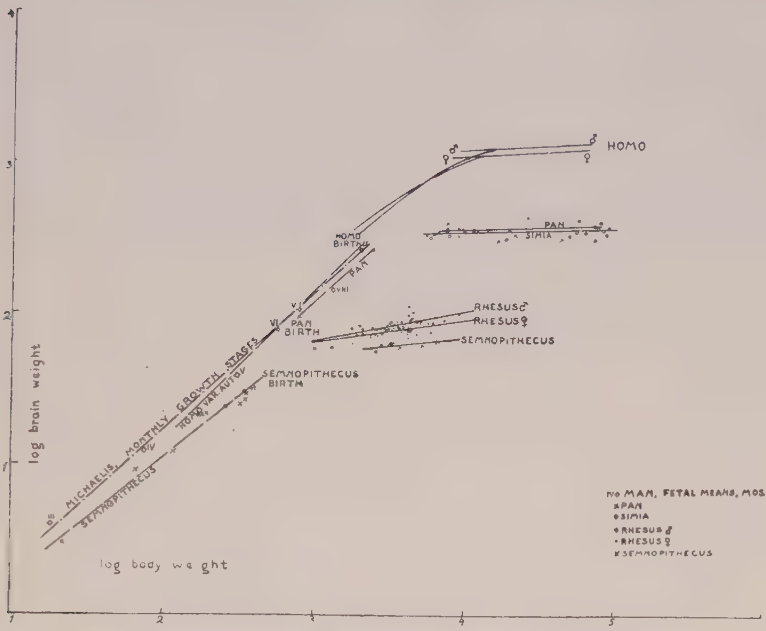


Figure 4. Primate ontogeny. Broken lines: prenatal; solid lines: postnatal.

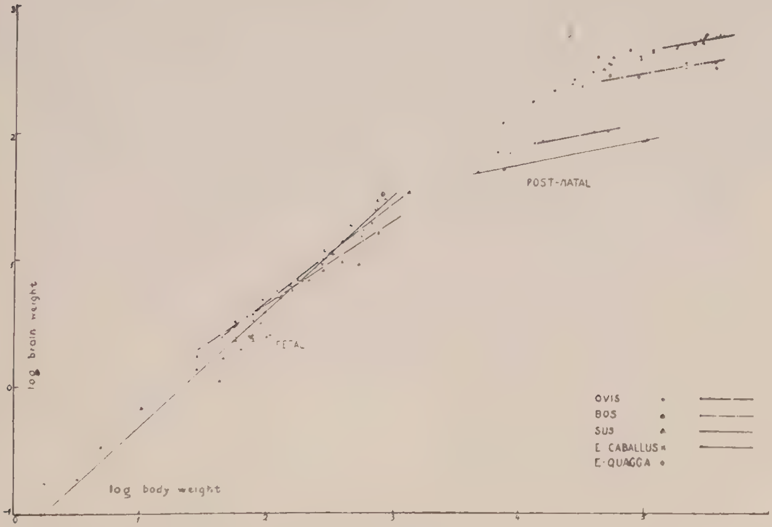


Figure 5. Ungulate ontogeny. Note the parallelisms, but also the different levels and lengths, of the postinfantile lines. This includes the perissodactyls.

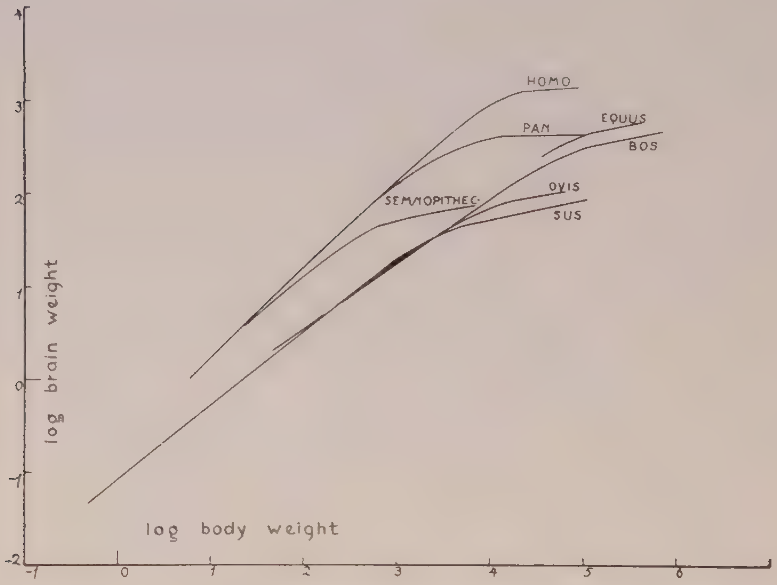


FIGURE 6. A comparison of ontogenetic curves of some primates and ungulates.

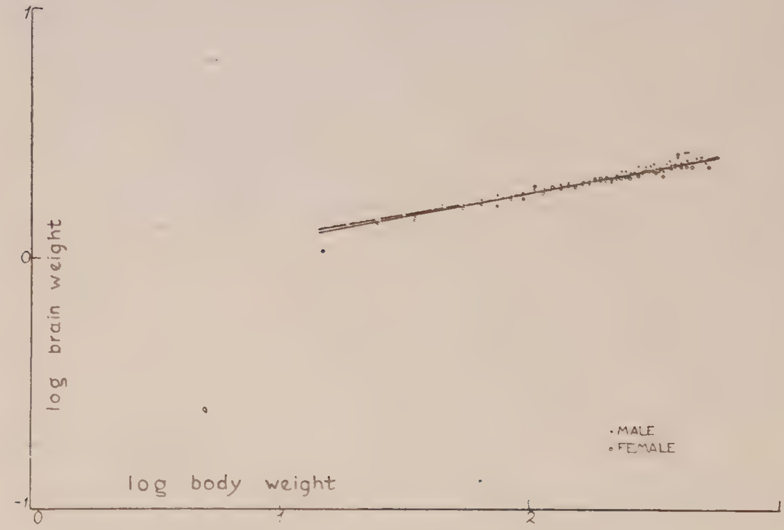


FIGURE 7. Postnatal growth of Norwegian rats.

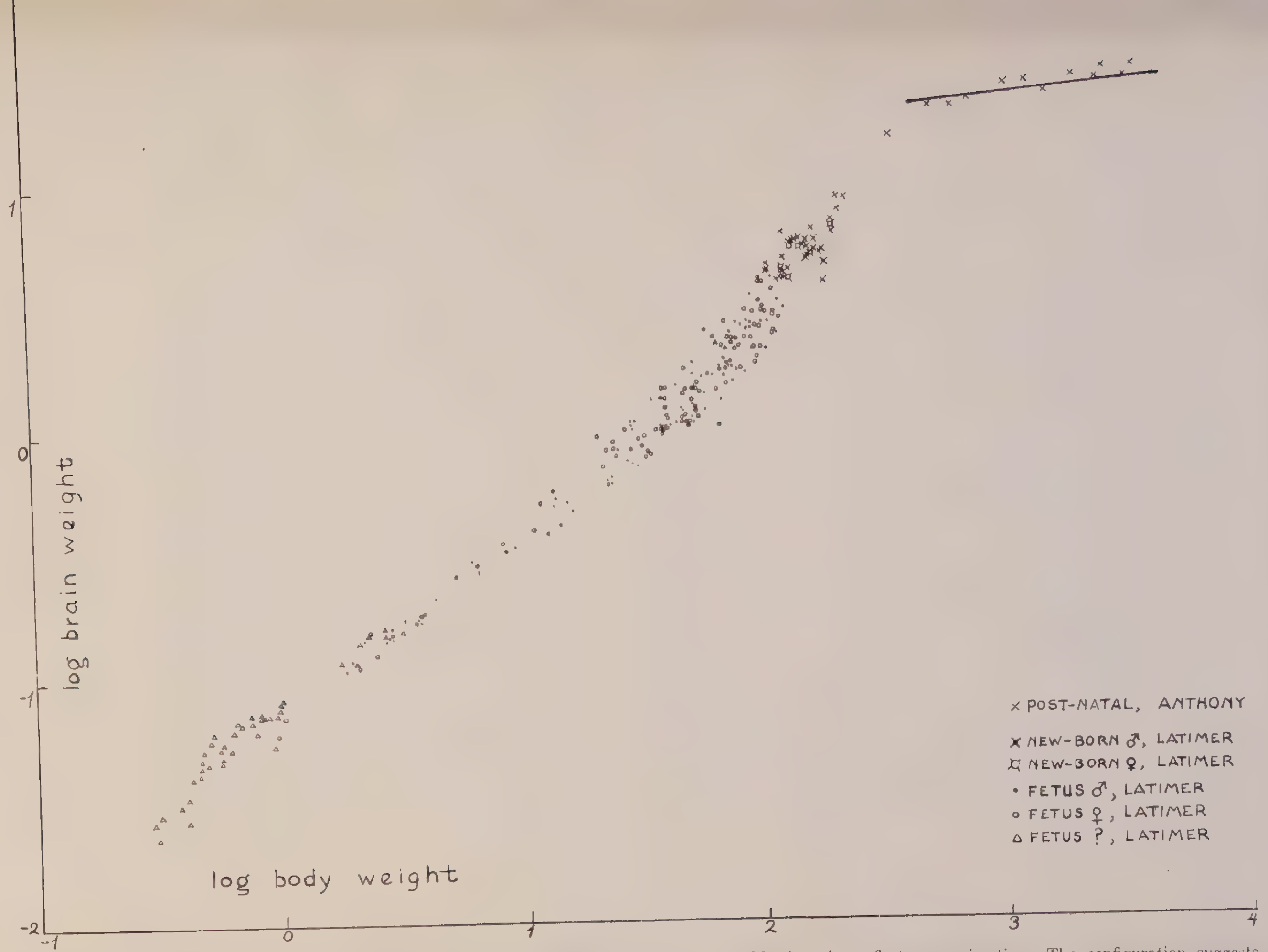


FIGURE 8. Ontogeny of the cat, to illustrate that the rectilinear fetal formula probably is only a first approximation. The configuration suggests, rather, a complex logistic, with the infantile axis of growth an inclined asymptote.

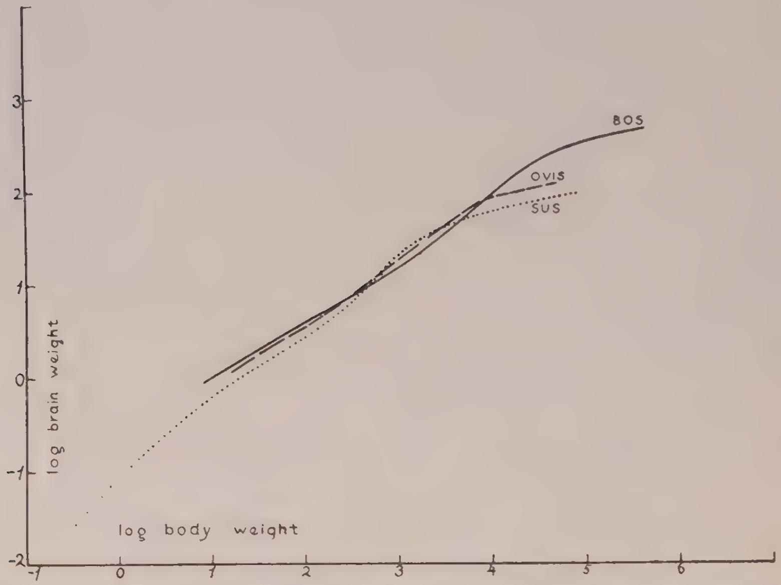


FIGURE 9. The ontogenesis of three artiodactyl genera to illustrate the presumably more correct morphology. This would make of the tabulated fetal formulae but first approximations. Suggested by a comparison of the data with those of **Latimer's** cats (FIGURE 8).

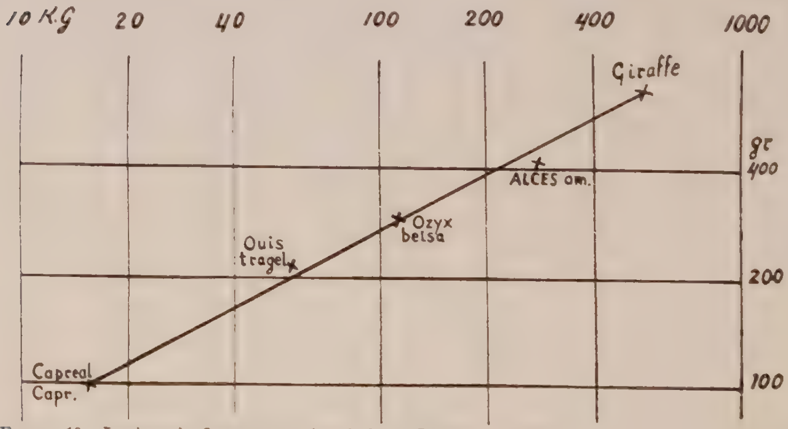


FIGURE 10. Lapicque's figure, reproduced from **Kappers** (1929), showing some Pecora genera fitted to a line $Y = A + .56\ X$. To illustrate Dubois' hypothesis.

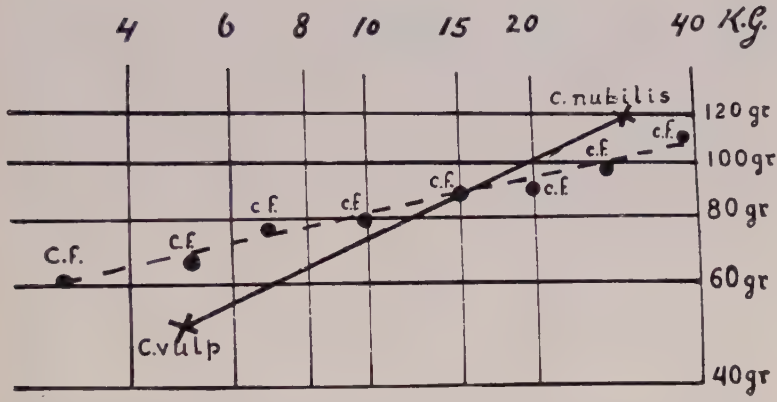


FIGURE 11. Lapicque's figure, reproduced from **Kappers,** showing a slope of approximately .25 fitted to graded sizes of *Canis familiaris* (c.f.), and intersecting a slope of .56 which joins two wild species of *Canis.*

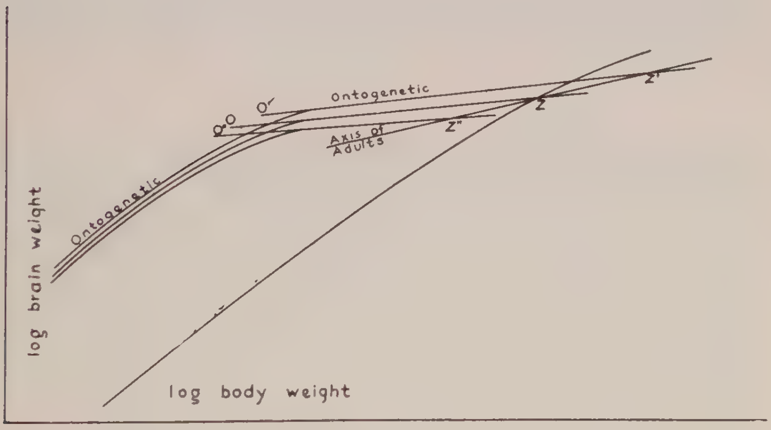


FIGURE 12. A putative explanation of the relationships, in a given species or genus, between ontogenetic curves, the axis of an adult constellation, and a parabolic cephalization exponent which is comparative anatomic. Of the ontogenetic curves, the central one represents the mean of the species. It is flanked by individuals respectively bigger and smaller than the average. The straight lines, OZ, etc., are postinfantile to adult, the curves being the postnatal infantile. The adult population, presumably, is oriented by the line Z″ZZ′; it has been drawn to a slope of about .23 (*cf.* **Lapicque**). The comparative-anatomic parabola, which is the central theme of Section IV, is steeper, and over a considerable stretch may approximate .56 as a slope; or (Primates) it may be steeper. It is not far from paralleling the fetal ontogenetic curve (see Section V and FIGURE 24).

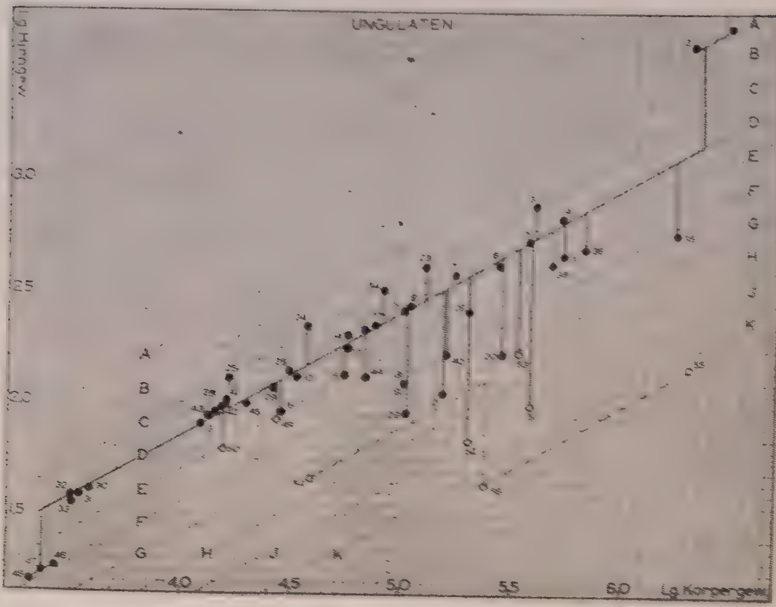


FIGURE 13. The ungulate scheme of **Brummelkamp** (1939c). See TABLE 13.

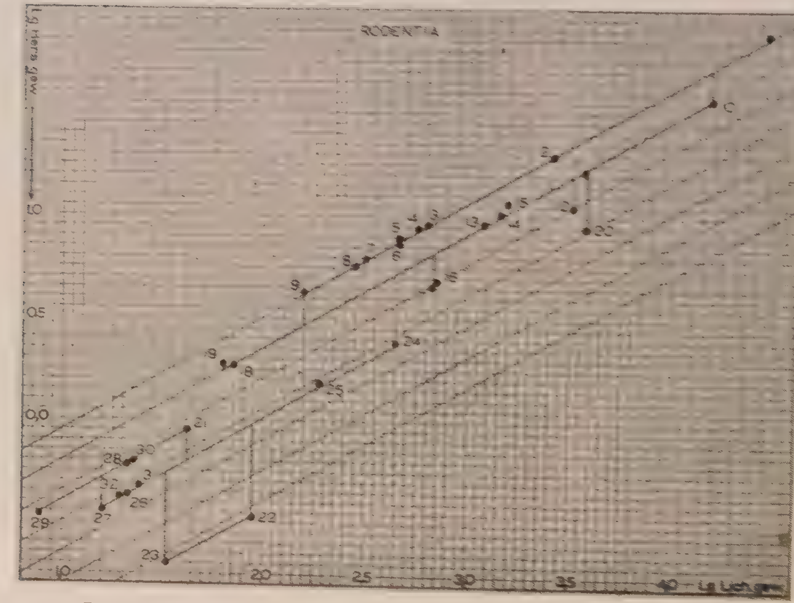


FIGURE 14. The rodent scheme of **Brummelkamp** (1939b). See TABLE 14.

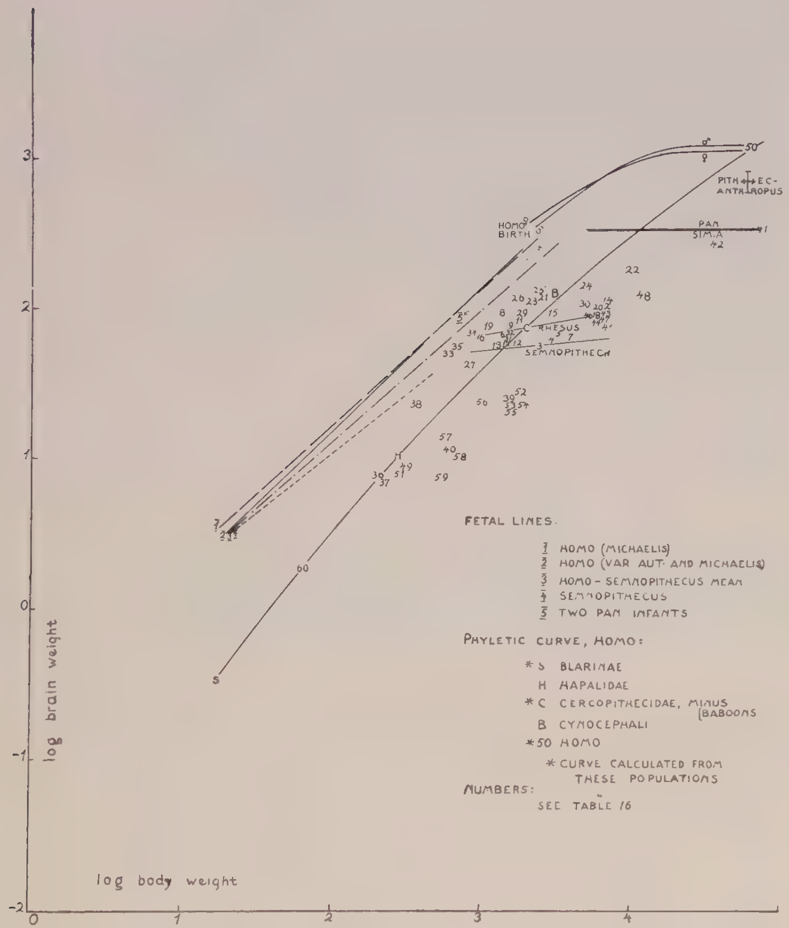


FIGURE 15. A synopsis of ontogenetic curves of *Homo*, *Semnopithecus* (and *Pan*), compared with the cephalization exponent of man (as developed in Section IV. See also FIGURE 24 and Section V). The numbers are the catalogue of TABLE 16.

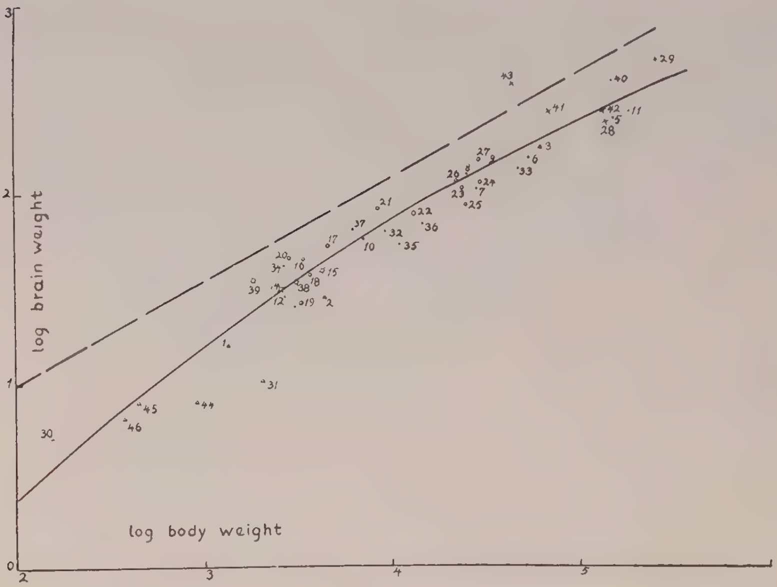


FIGURE 16. Detail of the Carnivora constellation, for comparison with FIGURE 18 (Artiodactyla). The straight, broken line has a slope of .56 and arbitrarily passes through $Y = 0$, $X = 0$. The parabola is formulated in TABLE 26. See TABLE 15 for key to entries.

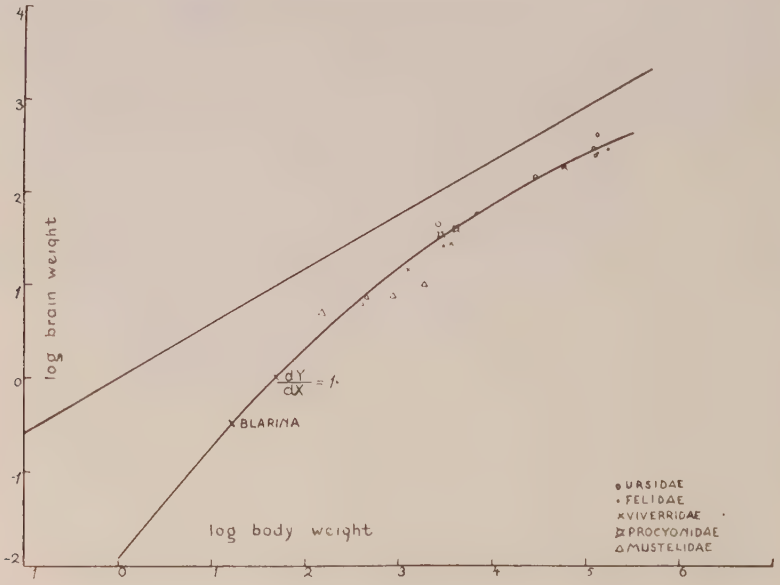


FIGURE 17. Cephalization exponent of the carnivores, calculated from *Blarina*, Mustelidae, and Procyonidae only. Note the fit of the other Carnivora, which have been entered upon the field merely as a check. For comparison with FIGURE 19 (Artiodactyla).

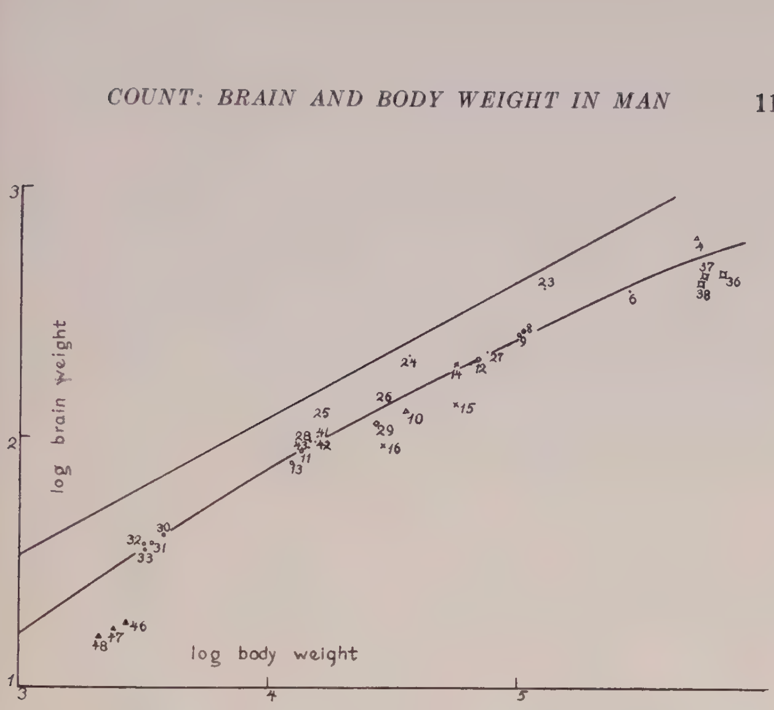


FIGURE 18. Detail from FIGURE 13. The numbering is by **Brummelkamp** (see TABLE 13). The straight line, like the slopes of Brummelkamp, has a slope of .56 and passes, arbitrarily, through $X = 0$, $Y = 0$. The curve has the parabolic formula No. 16 of TABLE 26.

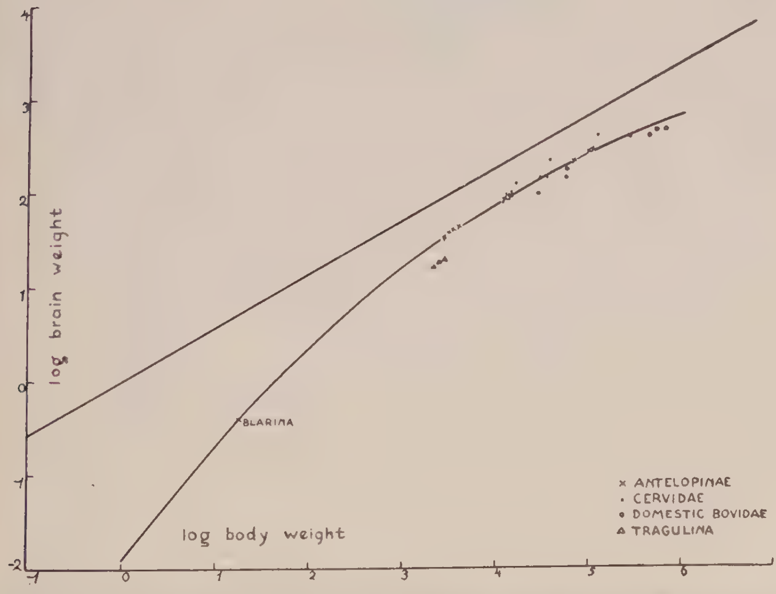


FIGURE 19. The cephalization exponent of the Antelopinae, calculated from *Blarina* and Antelopinae only. Note closeness of fit of the other artiodactyls. For comparison with FIGURE 17 (Carnivora). The rectilinear line slopes at .56, and arbitrarily passes through $Y = 0$, $X = 0$.

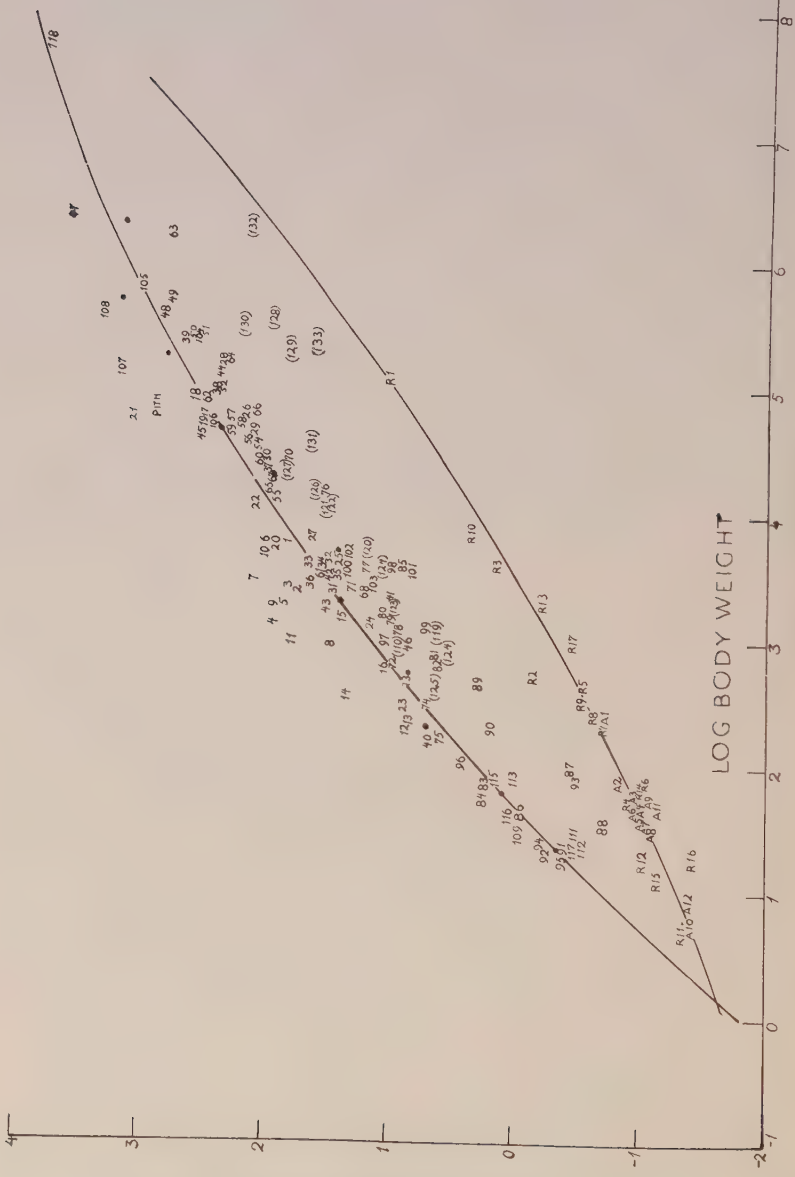


Figure 20. See opposite page.

FIGURE 20. The mean statistical tendency of extant Mammalia, (upper curve, concave downward) and that of extant Reptilia (lower curve, concave upward). Mammalian data from subjoined list; reptilian and amphibian, from TABLES 21 and 22. Plain numbers: mammals. "R" numbers: reptiles. "A" numbers: amphibia. The entries in parentheses are extinct mammals, and were not included in the calculation; neither were the marsupials, although extant and registered in the field. The black spots are means (dead centers) of the eleven areas of TABLE 25.

1 *Semnopithecus*
2 *Cercopithecus*
3 *Chlorocebus*
4 *Cercocebus*
5 *Macacus*
6 *Cynopithecus*
7 *Cynocephalus*
8 *Mycetes*
9 *Ateles*
10 *Lagothrix*
11 *Cebus*
12 *Hapale*
13 *Iacchus*
14 *Midas*
15 *Lemur*
16 *Nycticebus*
17 *Simia*
18 *Gorilla*
19 *Pan*
20 *Hylobates*
21 *Homo*
22 *Symphalangus*
23 *Oedipomidas*
24 *Genetta*
25 *Ichneumia*
26 *Crocuta*
27 *Felis*
28 *Felis*
29 *Felis*
30 *Felis*
31 *Potos*
32 *Procyon*
33 *Vulpes*
34 *Urocyon*
35 *Otocyon*
36 *Thos*
37 *Canis*
38 *Ursus*
39 *Thalarctos*
40 *Mustela*
41 *Mephitis*
42 *Nasua*
43 *Potos*
44 *Melursus*
45 *Helarctor*
46 *Putorius*
47 *Elephas*
48 *Camelus*
49 *Giraffa*
50 *Equus*
51 *Alces*
52 *Oryx*
53 *Antilope*
54 *Antilocapra*
55 *Antilope*
56 *Gazella*
57 *Ovis*
58 *Sus*
59 *Cervus*
60 *Rupicapra*
61 *Cephalophus*
62 *Damaliscus*
63 *Hippopotamus*
64 *Tapirus*
65 *Capreolus*
66 *Phacochaerus*
67 *Tayassu*
68 *Tragulus*
69 *(Zebra)*
70 *Hydrochaerus*
71 *Dasyprocta*
72 *Sciurus*
73 *Sciurus*
74 *Sciurus*
75 *Sciurus*
76 *Hystrix*
77 *Lepus*
78 *Lepus*
79 *Oryctolagus*
80 *Pteromys*
81 *Cavia*
82 *Cavia*
83 *Dipus*
84 *Sciuropterus*
85 *Lagostomus*
86 *Arvicola*
87 *Arvicola*
88 *Mus*
89 *Mus*
90 *Mus*
91 *Mus*
92 *Mus*
93 *Mus*
94 *Cricetulus*
95 *Mus*
96 *Geomys*
97 *Perodipus*
98 *Capromys*
99 *Fiber*
100 *Tamanduas*
101 *Dasypus*
102 *Choloepus*
103 *Bradypus*
104 *Erignathus*
105 *Odobenus*
106 *Phoca*
107 *Phocaena*
108 *Delphinapterus*
109 *Desmodus*
110 *Pteropus*
111 *Rhinolophus*
112 *Vespertilio*
113 *Tupaja*
114 *Erinaceus*
115 *Talpa*
116 *Scalopus*
117 *Blarina*
118 *Balaenaptera*
119 *Didelphis*
120 *Onychogale*
121 *Macropus*
122 *Petrogale*
123 *Trichosurus*
124 *Trichosurus*
125 *Dasyurus*
126 *Thylacinus*
127 *Mesohippus*
128 *Paleosyops*
129 *Anoplotherium*
130 *Moeritherium*
131 *Diplobune*
132 *Uintatherium*
133 *Coryphodon*

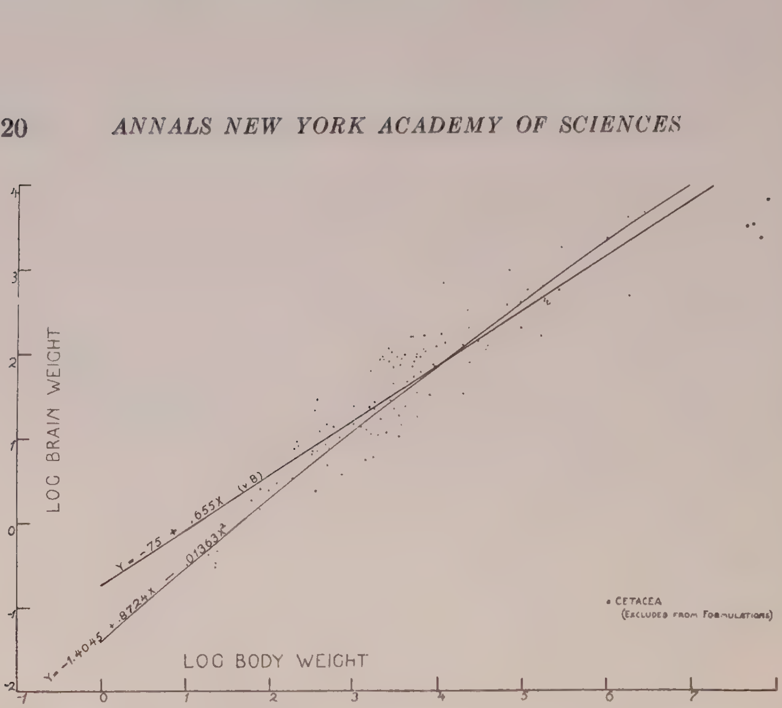


FIGURE 21. Mammalian constellation of **von Bonin,** fitted with his regression line, and a parabola, calculated as *a*, explained in the text. Compare with FIGURE 20. The straighter character of the parabola in the present case is due, in part at least, to the exclusion of the giant Cetacea from the data. This was not done in FIGURE 20.

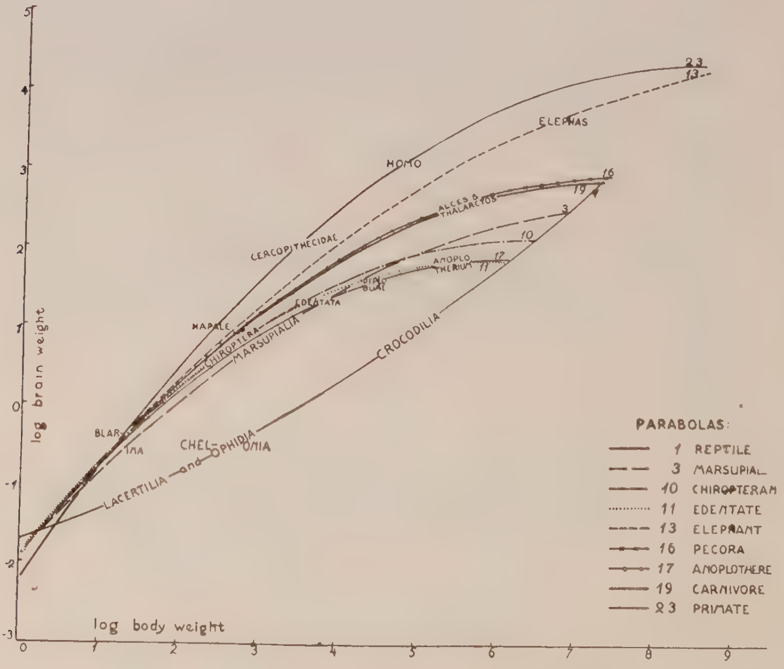


FIGURE 22. Some exponents of cephalization drawn from formulae of TABLE 26, and numbered accordingly. The parabolas pass indefinitely; a very few genera, orders, etc., have been placed in the region where they occur, as guides to visualization.

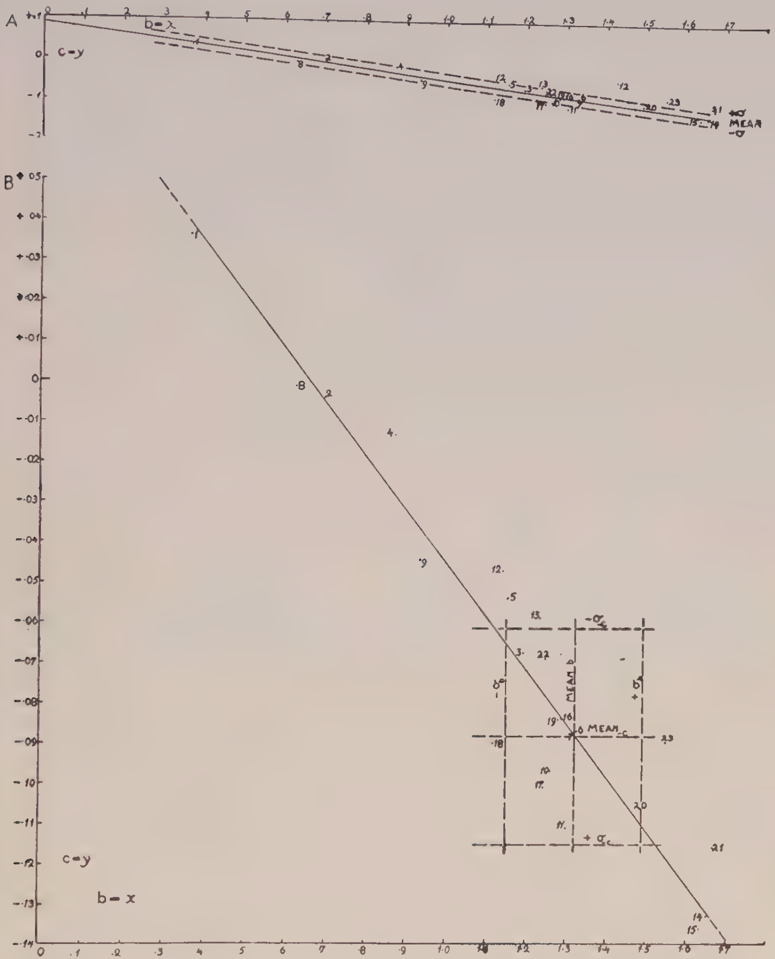


FIGURE 23. Plot of b as x and of c as y, from the parabolas of TABLE 26. Entry numbers accordingly. In A, the scales are the same; in B, the ordinate scale has been multiplied by 10. In A, the broken lines are the $\pm\sigma$ limits if all points are projected on to a common line placed normal to the line of the mean. In B, the broken-line rectangle limits the $\pm\sigma$ of mean b and of mean c, respectively. This illustrates the degree of "typicalness" of each of the parabolas of TABLE 26, when the mean of all *surviving* cephalization exponents, regardless of the absolute brain and body weights of the genera that they characterize, is taken as standard.

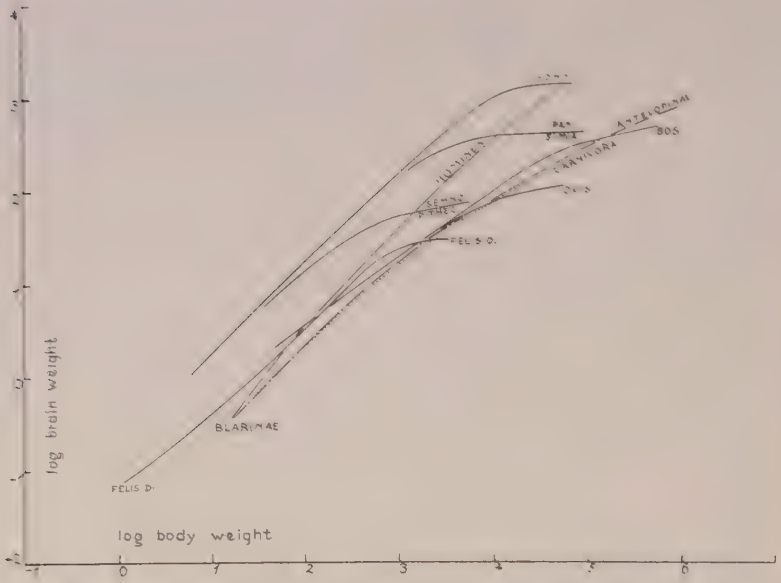


FIGURE 24. Synoptic comparison of ontogenetic and comparative-anatomic curves of some genera-orders. Solid lines: ontogenetic: broken lines: comparative-anatomic. Note parallelisms between fetal and comparative-anatomic trends, yet with fetal always showing a brain precocity. Compare with FIGURE 12.

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